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Dietary Shifts, Niche Relationships and Interspecific Competition in Sympatric Grey Langur (Semnopithecus entellus) and Purple-faced Langur (Trachypithecus vetulus) in Sri Lanka

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Dietary Shifts, Niche Relationships and Interspecific Competition in the Sympatric Grey Langur (*Semnopithecus entellus*) and the Purple-Faced Langur (*Trachypithecus vetulus*) in Sri Lanka

by

Rajnish Vandercone

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Abstract of the dissertation

Dietary shifts, Niche Relationships and Interspecific Competition in the Sympatric Grey Langur (*Semnopithecus entellus*) and the Purple-Faced Langur (*Trachypithecus vetulus*) in Sri Lanka

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Professor David T. Rasmussen, Co-Chairperson

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Understanding how niche differences evolve in ecologically similar species and how these differences are maintained ecologically is a fundamental question in ecology. Interspecific competition has been shown to influence the behavior and ecology of organisms in a wide range of ecological communities. However, the broader role of interspecific competition in primate communities is unclear as relatively few studies have explored this question. This is especially true for folivorous primate communities, such as those of colobine monkeys, in which the influence of interspecific competition on aspects of the ecology of these monkeys is yet to be determined.

In this dissertation, I present data and analyses on the dietary ecology, ranging behavior, and interspecific interaction in *Trachypithecus vetulus* and *Semnopithcus entellus.* I use this work to assess the possible role of interspecific competition on the behavior and ecology of these species. I specifically explored this issue by investigating: 1) the monthly variation in dietary overlap in relation to monthly resource availability, 2) interspecific interactions in relation to resource availability, 3) the influence of interspecific interaction on feeding effort, and 4) the influence of interspecific interaction on vertical habitat use patterns. In this study, both species showed similar feeding patterns when feeding on seasonal plant items, but showed a preference for fruit and flowers over leaves, a trend not reported in previous studies on these species. The langurs in this study also consumed a high proportion of flowers in comparison to other colobine monkeys, making this population one of the most florivorous colobine populations. In addition, both species preferred to feed on tree species that were relatively rare and showed clumped distributions. Clumped resource distributions have been suggested to promote within-group and interspecific competition.

Home range overlap between *T. vetulus* and *S. entellus* was extensive. Although resource availability within the home ranges of *S. entellus* and *T. vetulus* were similar, the index of defendability (*D*) of *S. entellus* was higher than the index of defendability (*D*) of *T. vetulus*. This suggests that the two groups of *S.entellus* traversed their home range more intensely than *T. vetulus*. *Trachypithecus vetulus* travelled a relatively short distance on any given day in comparison to *S. entellus* and consequently utilized only a fraction of its total home range.

The dietary overlap between *S. entellus* and *T. vetulus* showed considerable temporal variation in comparison to dietary overlap between other closely related primate species. There was no significant relationship between monthly dietary overlap of immature leaves and monthly immature leaf availability. However, dietary flower overlap was high during periods of flower availability and low during periods of flower scarcity. This observation was consistent with observations from other studies, which show competitors to reduce diet overlap in response to the decline in resources. On the contrary, dietary fruit overlap tended to be high during periods of fruit scarcity as both species converged on the same fruit tree species. However, these primates were never observed to occupy feeding trees at the same time. Interactions between *S. entellus* and *T. vetulus* occurred mostly during the period when fruit availability was low. These interactions resulted in a reduction in the proportion time devoted to feeding by *T. vetulus*. In addition, during these interactions *T. vetulus* was displaced from feeding trees, which also resulted in *T. vetulus* altering its vertical habitat use pattern.

These observations demonstrate that *S. entellus* was dominant over *T. vetulus* during intergroup interactions and hence it is possible that the low level of mobility and the low intensity of home range use observed for *T. vetulus*, and dietary niche partitioning by these species are adaptations by these primates to mitigate ecological competition and promote coexistence.

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Chapter 1

Introduction

1.1 Research objectives

Studies on competition in primates have predominantly focused on the influence of intragroup competition on primate socioecology. However, several lines of evidence demonstrate that interspecific competition may be an important factor in promoting and maintaining niche differences in sympatric primate species. These lines of evidence include work on saturated primate communities (Lawes and Eeley 2000), correlation between primate biomass and food supply (Davies 1994; Chapman et al. 2004), density compensation (Peres and Dolman 2000), positive correlation between ratios of body mass and the number of species at a site (Ganzhorn 1999), correlation between body size and dominance hierarchies in tropical frugivores (French and Smith 2005) and aggressive interactions between species (Stevenson et al. 2000). Despite this evidence, the broader role of interspecific competition in primate communities is still unclear as only a relatively few studies have addressed this topic precisely (Stevenson et al. 2000; Tutin et al. 1997; Guillotin et al. 1994; Gautier-Hion 1980). However, the majority of these studies failed to carry out empirical tests for competition and only considered one line of evidence, namely dietary overlap (Tutin et al. 1997; Guillotin et al. 1994; Gautier-Hion 1980). Since the relationship between dietary overlap and competition is unclear, the results of these studies are largely inconclusive.

Fieldwork was carried out to gather data on the ecology of *Trachypithecus vetulus* and *Semnopithecus entellus* in the north central dry zone forests of Sri Lanka during May-

July 2005 and July 2008-June 2009. The objective of this study was to examine food resources and habitat use of these two sympatric Asian colobine monkeys to assess whether interspecific competition influences behavior and ecology in these species. The study was conducted at the Kaludiyapokuna forest reserve, a relatively undisturbed forest in the north central dry zone of Sri Lanka. The north central dry zone forests of Sri Lanka provided an ideal opportunity to study the interaction of these two species, which overlapped in their ranges in this region.

Observations were made on two groups of *S. entellus* and one group of *T. vetulus*. Data on feeding, habitat utilization, ranging and interspecific interaction were collected to test predictions based on competition theory. A number of studies have demonstrated sympatrically occurring ecologically similar species to diverge in their diets in response to the reduction of resource availability (Schoener 1986; Tutin et al. 1997; Guillotin et al. 1994). Such changes in overlap have been suggested to reflect the intensity of interspecific competition (Korpimaki 1987). Based on the outcome of these studies, it was predicted that if these two species compete for food, the diet overlap (degree of resource partitioning) between these two species should be the greatest during periods when fruit, flowers and immature leaves are abundant and reduced during periods when resources are scarce.

Interference competition has also been shown to influence aspects of the ecology of species such as habitat use (Brown 1971) and foraging effort (Ziv and Kotler 2003; French and Smith 2005). It was predicted that if interference competition is an important interaction, interspecific encounters should occur during the phases when preferred, limited, patchily distributed resources such as fruit and flowers are low in availability. In addition, a comparison of the feeding rates when the two species were in association and when they were not was also proposed. If competition occurred and one species displaced the other from feeding sites, it was predicted that the feeding rates of one or both species would be lower when in association than when they were not.

Studies that contrast the niches of species in the presence and absence of competitors have shown species to alter their habitat preferences in response to the presence of competitors (Huey et al. 1974; Schoener 1975; Diamond 1978; Alatalo et al. 1985). To investigate the influence of interspecies interaction on habitat use patterns of these primates, a comparison of the vertical dispersion of the two species when they were in close association *versus* when they were not was also examined.

The data presented in this dissertation addresses a number of theoretical issues relating to the importance of interspecific competition in foli-frugivorous primate communities. In addition, the data on group structure, feeding ecology, ranging and habitat use presented here broadens and furthers the understanding of the ecology of these species and the Colobinae in general. These data are also invaluable to the conservation of these species as information based on systematic data collection is sparse for these primates in Sri Lanka. Gathering information on these species has become of increased importance as Sri Lanka has one of the highest rates of deforestation in Asia (Dinerstein and Wikramanayake 1993) and is the global biodiversity hotspot that has the highest category of population pressure (Cincotta et al. 2000). Currently, *Semnopithecus entellus thersites* and *Trachypithecus vetulus* are classified as endangered in the International Union for

Conservation of Nature (IUCN) red list of threatened species (IUCN 2011). *Trachypithecus vetulus nestor,* a distinct population inhabiting the Western Province of Sri Lanka, had also been listed as on of the world's 25 most endangered primates (Mittermeier et al. 2009).

1.2 Theoretical background

Numerous authors have acknowledged the existence of regular patterns within communities such as distribution complementarities (Gilpin and Diamond 1982), resource partitioning and the temporal variation in the degree of resource partitioning (Schoener 1986; Korpimaki 1987), character displacement (Brown and Wilson 1956), habitat shifts (Schoener 1975; Diamond 1978) and niche expansion (Lister 1976). Interspecific competition has been frequently identified as the chief agent responsible for establishing these patterns in ecological communities (Pacala and Roughgarden 1985; Gurevitch et al. 1992). Competition has been shown to alter population densities (Hairston 1951), foraging efficiency, growth rate (Dunham, 1980; Gustafsson 1987; Ziv and Kotler 2003), age structure (Smith 1981), habitat use (Creel and Creel 1996), and activity patterns (Kotler et al. 1993; Jones et al. 2001), and is widely regarded as one of the important interactions and holds a central place in ecological and evolutionary theory (MacArthur and Levins 1964, 1967; Gurevitch et al. 1992).

The concept of ecological competition or “the struggle for existence” was first formulated by Darwin as an integral component of the theory of natural selection. In 1859 Darwin wrote:

As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera. We see this in the recent extension over parts of the United States of one species of swallow having caused the decrease of another species. (p.76)

In 1934 the experiments carried out by the Russian scientist G. F. Gause re-emphasized Darwin's struggle for existence. These classic experiments were performed using two species of protozoans, *Paramecium aurelia* and *Paramecium caudatum.* Initially the two species were placed into culture media that were maintained under identical conditions. Under these conditions each species exhibited normal growth patterns and reached equilibrium. However when both species of paramecium were placed in the same culture, *Paramecium caudatum* was exterminated and only *Paramecium aurelia* survived after sixteen days. Neither organism attacked the other or secreted harmful substances. *Paramecium aurelia* had a higher rate of increase in comparison to *Paramecium caudatum*, and consumed more of the limited amount of food available in the culture. In further experiments, Gause placed the loser, *Paramecium caudatum*, with another species, *Paramecium bursaria*. These two species were able to coexist because *P.caudatum* fed on the bacteria suspended in the solution, whereas *P. bursaria* fed on the bacteria at the bottom of the tubes. Through his experiments Gause illustrated that two species with similar ecological requirements could not coexist in the same environment. This theorem has been referred to as Gause's law or the principle of competitive exclusion.

1.2.1 Tests of competitive exclusion

Since Gause's work, similar experiments have been carried out by numerous other investigators. Thomas Park (1948; 1954) used two species of flour beetles *Tribolium confusum* and *Tribolium castaneum* in a controlled lab setting. In the absence of the parasitoid *Adelina*, *Tribolium confusum* was driven to extinction. In the presence of the parasitoid, *Tribolium castaneum* became extinct. Park (1948; 1954) also demonstrated that the outcome of competition between the two beetles depended upon environmental temperature, humidity and on the fluctuations in the total number of eggs, larvae, pupae, and adults. Often the outcome of competition was not determined for generations. Laboratory experiments carried out by other investigators also confirm Gause's hypothesis that two species with similar ecological requirements cannot exist in the same environment (Crombie 1946; Frank 1957). Apart from these laboratory experiments there are also numerous field experiments and observations that lend support to the principle of competitive exclusion (Connell 1961; Brown 1971; Jaeger 1971) However most of the cases of competition exclusion in nature are based upon circumstantial, distributional evidence, and only Connell (1961) and Brown (1971) proposed mechanisms of exclusion. Connell (1961) performed field experiments on two species of barnacle: *Chthamalus stellatus* and *Balanus balanoides*. Adult *Chthamalus stellatus* occurred in the marine intertidal zone above that of *Balanus balanoides*. *Chthamalus* was never able to establish itself in the zone where *Balanus* occurred because *Chthamalus* settled in much smaller numbers in comparison to *Balanus*. Also, when *Chthamalus* settled, *Balanus* smothered, undercut, or crushed the *Chthamalus*. The greatest mortality of *Chthamalus* occurred during the season of most rapid growth of

Balanus. Brown (1971) described the interactions between two species of chipmunks (*Eutamias dorsalis* and *Eutamias umbrinus*), which excluded each other from certain latitudinal ranges on numerous mountain peaks in the central Great Basin. *E. dorsalis* excluded *E. umbrinus* from sparse piñon-juniper forests at lower elevations and *E. umbrinus* excluded *E. dorsalis* from denser forests in high altitude. However the two species overlapped in a narrow strip of intermediate habitat. In this region *E. dorsalis*, the more aggressive and terrestrial of the two species chased *E. umbrinus* from areas where the trees were widely spaced. The competitive advantage shifted to the more arboreal and social *E. umbrinus* when the trees were sufficiently large and dense that their branches interlocked. In these habitats *E. umbrinus* readily escaped *E. dorsalis* by fleeing through the trees over routes that the *E. dorsalis* could not follow. In such situations the aggressive nature of *E. dorsalis* was counterproductive because *E. umbrinus* was so numerous that that latter wasted a great deal of energy on chases. The differences between the two species in aggressive behavior apparently represent responses to the density of cover and food resources in their habitats.

In addition to these examples from the laboratory and the field, examples are also available from areas in which new species have been recently introduced. The introduction of the American grey squirrels into several regions in Briton at the end of the 19th Century has caused the disappearance of red squirrels, *Sciurus vulgaris*, throughout much of their geographic range (Lloyd 1983; Usher et al. 1992). The grey squirrels are less arboreal, digest acorns more efficiently, and put on more weight over winter than red squirrels (Kenward and Holm 1993). These differences probably give grey squirrels a competitive advantage in deciduous woodlands (Kenward and Holm 1993). Similarly the human-aided invasion of urban/suburban areas by the sexual gecko *Hemidactlylus frenatus* has caused the decline of the native asexual gecko *Lepidodactylus lugubris* throughout the Pacific (Petren and Case 1996). *Hemidactlylus frenatus* depleted insect resources to lower levels than *Lepidodactylus lugubris*, which resulted in reduced resource acquisition in *Lepidodactylus lugubris.* Reduced resource acquisition translated into reductions in the body condition, fecundity, and survivorship of *Lepidodactylus lugubris* (Petren and Case 1996).

In all of the above examples exclusion occurs or is assumed to occur as a result of the species concerned competing for identical environmental resources. Since these observations and many others support Gause's original conclusion, the principle of competitive exclusion has been widely regarded as an important principle of community ecology.

1.2.2 Community and guild structure

Competition holds a central place in ecological and evolutionary theory and has been perceived as an important determinant of community and guild structure (MacArthur and Levins 1964, 1967; Schoener 1983; Gurevitch et al. 1992). In a meta-analysis of field experiments on competition by Gurevitch et al. (1992), competition was found to have the largest effect overall on the biomass of 93 species in a wide range of habitats. Field experiments have revealed a wide range of competitive effects on populations of organisms. Experiments by Dunham (1980) on two iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus* showed that individual foraging success, growth rate, body mass, prehibernation lipid levels, and population densities, were significantly lower in the control populations of both species during dry years, indicating that both species experience stressful conditions during dry years. Arthropod abundance was found to be low during dry years. In the experimental plots where *Sceloporus merriami* was removed, the density, individual foraging success, growth rate, prehibernation body mass, and lipid levels of *Urosaurus ornatus* were significantly greater than in the control populations. Similar experiments on *Sceloporus merriami* and *Urosaurus ornatus* showed that the age structure of the population was affected by age specific competition during the dry season (Smith 1981). In both species the survival of yearling females was significantly greater in experimental plots. Experiments on Great Tits, Blue Tits and Collared Flycatchers showed that the two tit species had negative effects on the fitness of Collared Flycatchers (*Ficedula albicollis*) possibly through competition for food during both the nestling and post fledging periods (Gustafsson 1987). When densities of tits were experimentally reduced, the number and mass of Collared Flycatcher fledglings increased in comparison with those in experimental plots (Gustafsson 1987). In addition to direct effects of competition, competitive interactions between species may have an effect on the vegetation of the habitat and in turn indirectly affect other species in the habitat. Such indirect effects are probably more widespread and important in structuring communities (Heske et al. 1994). Brown and Davidson (1977) carried out experiments on competitive interactions between rodents and ants during which rodents and ants increased in response to the absence of the other taxon. Also the analysis of the soil revealed that the density of seeds was 5.5 times greater and the densities of annual grasses (*Bouteloua barbata* and *B. aristidoides*) was 2.0 times greater on plots from which rodents and ants were absent in comparison to other plots in which rodents, ants or both were present.

Experiments carried out on rodents in the Chihauhuan Desert revealed that rodent abundance was influenced by direct competition and by indirect effects (Heske et al. 1994). Exclusion of kangaroo rats from study plots saw an increase in abundance of other species of rodents, produced dramatic changes in the relative abundance of several species and later caused major changes in the vegetation cover, particularly that of certain grasses (Brown and Heske 1990; Heske et al. 1994). The distribution of harvest mice were directly influenced by kangaroo rats by direct competition and indirectly by modifications caused to the habitat (Heske et al. 1994). The increase of cotton mice was entirely due to the increase in grass cover (Heske et al. 1994). These studies show interspecific competition to directly and indirectly influence the life history of organism and thereby the relative abundance of organisms in a habitat.

In addition to competition, other biotic and abiotic interactions such as mutualism (van der Heijden et al. 1998; Stachowicz 2001), predation (Turner and Mittleback 1990), climatic effects (Weins 1977) and heuristic theories such as neutral theory (Hubbell 2005) have been shown to successfully predict relative abundance and distributions of species in ecological communities and hence the relative importance of competition has been debated in recent years (Stachowicz 2001; Hubbell 2005).

1.2.3 Competition and conservation

Competition may also have implications for conservation. Some species are rarer than others in a given habitat. African wild dogs are endangered largely because their population density is low under all conditions (Creel and Creel 1996). Interspecific competition (interference) with larger carnivores like lions and hyaenas may be a factor limiting wild dog populations (Creel and Creel 1996). Hyaenas steal wild dog prey and as a result there is a strong negative correlation between wild dog densities and hyaena densities (Creel and Creel 1996). Similarly cheetahs (*Acinonyx jubatus*) in the Serengeti are limited by poor recruitment due to predation by lions and are found at higher densities outside protected areas than within (Caro and Laurenson 1994). Thus, limitations by larger carnivores (competitively dominant) may be an issue of general importance in conserving medium-sized carnivores (Creel and Creel 1996).

1.2.4 Definitions

Interspecific competition is a biotic interaction between two or more species, where one species may affect the population dynamics and carrying capacity of another, either through its effect on shared resources or by direct interference (Ricklefs 1990). Exploitative competition is similar to scramble competition where individuals use resources and deprive others of benefits to be gained from those resources. Exploitative competition associated with food resources is also defined as consumptive competition (Schoener 1983). Interference competition like contest competition involves individuals harming one another by fighting or producing toxins. Schoener (1983) defined four forms of interference competition: overgrowth competition, chemical competition, territorial competition and encounter competition. Overgrowth competition occurs when another individual or individuals grow over or upon a given individual, thereby depriving that individual of light or access to food and possibly harming that individual by some consequence of physical contact. Chemical competition occurs when an individual produces some chemical, which harms other individuals. Encounter competition occurs as a result of an interaction between mobile individuals in which some harm comes to one or more. Harm can include time or energy losses, theft of food, injury, or death by predation, fighting, or mere accident. Territorial competition occurs mainly in mobile organisms, when an individual aggressively defends, or by its behavior signals its intention to defend, a unit of space against other individuals. An analysis of experiments on competition revealed that consumptive competition and territorial and encounter competition are common among terrestrial animals (Schoener 1983). Territorial or encounter competition was the most common mechanism in most of the experiments involving birds and mammals and took the form of aggression or avoidance (Schoener 1983). It is often argued that certain interference mechanisms, especially territoriality are adaptations to secure food (Schoener 1983).

1.2.5 Models of coexistence

The principle of competitive exclusion is perceived as an impediment to species coexistence and community diversity and has been the catalyst for studies examining the conditions under which coexistence of interacting species is possible (Chesson and Huntley 1997). Several conditions such as spatial heterogeneity (Atkinson and Shorrocks 1981; Hanski 1994; Rees et al. 1996), temporal heterogeneity (Huston 1979; Menge 1979; Chesson and Warner 1981) and resource partitioning (MacArthur and Levins 1967) have been proposed to explain species coexistence and community diversity.

Environmental heterogeneity refers to the existence of different states or conditions which organisms must adapt to and exploit if they are to persist in the environment (Tokeshi 1999). Environmental heterogeneity in space and time is the result of both abiotic and biotic processes, the relative strengths of which are variable depending on the spatio-temporal scales involved (Tokeshi 1999). The impact of spetial heterogeneity on coexistence is illustrated by the work of Atkinson and Shorrocks (1981; 1984). Many insect species lay eggs in breeding sites such as dung carrion, fruit and fungi. Often it has been shown that several species of insects converge on a single type of breeding site and yet do not exclude each other despite strong competition between the larvae. Atkinson and Shorrock (1981) suggested an explanation for this using a simulation model. According to the model coexistence is partly possible by dividing the resource into more and smaller breeding sites, but equilibrium requires that the larvae of the superior competitor be aggregated independently of those of the inferior competitor. The aggregation of the larvae of the superior competitor into a few rather crowded breeding sites creates refuges in low density sites where the weaker species is safe from competition. Atkinson and Shorrock (1984) provided empirical evidence for the model by carrying out experiments on fruit breeding dipterans. The field data show that a large number of fruit breeding dipterans had aggregated distributions (Atkinson and Shorrock 1984). Although the model explains the coexistence of fruit flies and similar organisms, there is controversy over the aggregation mechanisms that are conducive to coexistence. Atkinson and Sharrock (1984) stated that female flies visit sites at random and lay clutches of random size giving rise to aggregated distributions. However, Green (1986) argued that most insect data and the biological mechanisms that they suggested do not satisfy the conditions of their model and do not lead to competitive coexistence. Green (1986) also suggested that coexistence may occur if aggregation results from a combination of mechanisms including resource partitioning.

Temporal heterogeneity can also promote coexistence is central to the non-equilibrium view of ecological communities. Temporal heterogeneity implies that different environmental conditions exist at temporally discrete intervals in the same locality (Tokeshi 1999). Some researchers suggest that environmental fluctuations (seasonal variation, weather etc.) disrupt equilibria and prevent consistent effects of competition (Hutchinson 1961; Weins 1977; Huston 1979). The work of Grover (1988) and others provide empirical evidence for this view. Grover (1988) used phosphorous limited continuous cultures to examine the hypothesis that environmental variability promotes coexistence of two species of phytoplankton *Synedra* sp. and *Fragilaria crotonensis* using. Variability was introduced into the system as a series of phosphorous pulses, which were delivered every eight days. The growth of the two species was examined in cultures of natural phytoplankton, in cultures containing both species but no other phytoplankton, and in monocultures. The experiment revealed that *Synedra* was competitively dominant to *Fragelaria* in both constant and varying cultures. However the rate of exclusion was comparatively slower in varying cultures. Although the idea may apply to a wide range of species assemblages, the exact mechanisms through which environmental fluctuations enhance coexistence are somewhat unclear (Tokeshi 1999). The work of Chesson and Huntly (1997) showed that the effects of competition are not diminished in the presence of harshness or fluctuations. They show that harshness makes a population less tolerant of competition because a population subject to harsh environmental conditions can have a negative growth rate and become extinct at lower levels of competition. Chesson and Huntly (1997) also suggested that coexistence under fluctuating environments can only be favored when fluctuations create spatial or temporal niche opportunities.

The most frequently cited studies of coexistence are those in which two or more species persist in the same area but are adapted to exploit different resources, and such studies are termed studies of resource partitioning. Resource partitioning generally refers to the state of reduced overlap in resource use between coexisting species and helps to alleviate potential competitive interactions (Tokeshi 1999). Hence many studies have focused on resource partitioning as a crucial mechanism, which underlies the coexistence of species in different communities. Pianka (1969) broadly categorized resource partitioning patterns into three general types: habitat, food type and time. From a historical perspective, the work by Lack (1947) on Darwin's finches of the Galapagos Islands could be considered important. Lack (1947) showed that the bill sizes of three species of Darwin's ground finches of the genus *Geospiza* differed greatly and ate seeds of different hardness and size. Ashmole (1968) studied 5 species of Christmas Island terns *Sterna fuscata*, *Anous stolidus*, *Gygis alba*, *Anous tenuirostris* and *Procelsterna cerulean* and observed that bill thickness was correlated with the food size. *Procelsterna cerulean* the species with the smallest bill cross-sectional area, consistently consumed fish less than 2 cm in length. *Anous tenuirostris* and *Gygis alba,* the two species with intermediate bill thickness consumed fish ranging from less than 2 cm to 8 cm length. However the percentage of fish less than 2 cm in length in their diet was significantly less in comparison to *Procelsterna cerulean*. *Anous tenuirostris* differed from *Gygis alba* in taking few fish more than 4 cm long. The two tern species with the greatest bill thickness, *Sterna fuscata* and *Anous stolidus* consumed fish ranging less than 2 cm to 12 cm but both species consumed few fish less than 2 cm in length in comparison with the tern species with medium and thin bills. Also *Anous stolidus* consumed a higher percentage of fish between 2 cm and 4 cm and longer than 10 cm in length than *Sterna fuscata*.

Four species of *Anolis* lizards, *Anolis sagrei*, *Anolis distichus, Anolis angusticeps,* and *Anolis carolinensis*, partitioned habitat according to perch height and diameter and food resources according to prey size and taxon (Schoener 1968). *Anolis sagrei* was partly terrestrial but often occurred on small and large low perches. *Anolis distichus* preferred tree trunks and large branches of medium to large trees. *Anolis angusticeps* was found to inhabit small twigs, especially at great heights and *Anolis carolinensis* was found to favor leaves or adjacent twigs and branches. In terms of prey size *Anolis sagrei* and *Anolis distichus* were found to be generalized while *Anolis carolinensis* and *Anolis angusticeps* were more specialized. In relation to prey taxa, *Anolis distichus* consumed a large proportion of ants and in terms of volume the dipterans were important. *Anolis sagrei* displayed a more generalized diet and included dipterans, aphids and beetles, termites and psocids. By volume Lepidoptera, plant material and beetles were found to be important. *Anolis sagrei* also consumed ants but considerably a lesser proportion in comparison with *Anolis distichus.* The diet of *Anolis angusticeps* was also found to be more diverse than that of *Anolis distichus* and predominantly included aphids and dipterans. By volume, Homoptera and Diptera were the major components of the diet. The Diptera, Hymenoptera (other than aphids) and winged Hymenoptera (other than ants) constituted the bulk of the prey items ingested by *Anolis carolinensis*. The former two categories and adult Lepidoptera contributed the greatest volume. A similar study on lizards was carried out on seven species of lizards in the genus *Ctenotus* (Pianka 1969). Larger species of

Ctenotus fed on larger food items than smaller ones. Also six species of *Ctenotus* did most of their foraging in open areas between plants, while six other species foraged within dense tussocks of porcupine grass (*Triodea* sp.) (Pianka 1969). In addition to separation in diet and habitat, temporal separation was also observed among certain species of lizards, noticeably in the case of *Ctenotus calurus* and *Ctenotus schomburgkii.*

Two species of stream dwelling chars *Salvelinus leucomaenis* and *Salvelinus malma* partitioned food resources according to prey size (Nakano et al. 1999). *Salvelinus leucomaenis* ate larger drift prey than *Salvelinus malma* when drift prey was abundant. Two species of sunfish *Lepomis macrochirus* and *Lepomis gibbosus* exhibited distinct diet and habitat separation in three small Michigan lakes (Mittelback 1984). *Lepomis macrochirus* foraged primarily on open-water zooplankton while *Lepomis gibbosus* specialized on vegetation-dwelling gastropods. The differences in resource use were directly related to differences in their functional morphology and foraging ability. *Myotis myotis* and *Myotis blythii*, two species of sympatric sibling bat species, were shown to coexist by habitat partitioning (Arlettaz 1999). *M. myotis* selected habitats that included freshly-cut meadows, intensively cultivated orchards and forest without undergrowth while grassland predominated in all habitats selected by *M. blythii*. Two rodents *Acomys cahirinus* and *A. russatus* occupied habitats that had similar characteristics, but *Acomys cahirinus* was more general in its habitat use and occupied a broader range of microhabitats (Jones et al. 2001). The two rodent species were also found to partition activity in the opposite parts of the diet cycle (Jones et al. 2001). *Acomys cahirinus* was found to be nocturnal and *A. russatus* diurnal, although it became nocturnal when its congener was experimentally removed (Jones et al. 2001). Similarly, two species of gerbils *Gerbillus allenbyi* and *Gebillus pyramidum* were also able to coexist through the temporal partitioning of resources (Kotler et al. 1993). *Gebillus pyramidum* foraged significantly earlier in the night than *Gerbillus allenbyi* and the last forage for *Gerbillus allenbyi* was significantly later than for *Gerbillus allenbyi*.

Five species of sympatric lorisids, *Perodicticus potto*, *Arctocebus calabarensis*, *Galago demidoff*, *Galago alleni*, and *Euoticus elegantulus* in Gabon were found to coexist by partitioning resources and habitat (Charles-Dominique 1974). *Perodicticus potto,* weighing 1100 g was found to be an exclusive climber, occupying the canopy in primary and secondary forest. The diet of *Perodicticus potto* consisted of 10% animal prey, 65% fruit and 21% gums. *Perodicticus potto* obtained most of its fruit from the canopy layer. *Gallago alleni*, the most frugivorous of the species, consumed 73% fruit and 25% animal prey and was restricted to primary forest and was found at heights ranging from 0-2 m. *Gallago alleni* collected its fruit mainly from the ground. The other species under study, *Arctocebus calabarensis* lived at heights ranging from 0-5 m both in primary and secondary forest. The diet of *Arctocebus calabarensis* consisted of 85% animal prey and 14% fruit. *Galago demidoff* occupied dense vegetation invaded by small lianas (35%) and foliage (25%) and was found at heights ranging from 10-30 m in primary forest and 0-10 m in secondary forest. *Galago demidoff* consumed a large proportion of animal prey (70%) and small quantities of fruit (19%) and gums (10%). *Euoticus elegantulus* scarcely descended to the ground and lived in the canopy up to 50 m. The diet of *Euoticus elegantulus* consisted of 20% animal prey, 5% fruit and 75% gums. Although both lorisines and galagines consumed insects as a part of their diet, 78% of the insect prey consumed by galagines consisted of beetles, nocturnal moths and grasshoppers, whereas the lorisines were specialized to tolerate noxious prey.

Similarly two species of Neotropical primates, Humboldt's woolly monkey (*Lagothrix lagothricha poeppigii*) and the white-bellied spider monkey (*Ateles belzebuth belzebuth*) were able to coexist by partitioning habitat and food (Dew 2005). The two species fed and foraged at significantly different heights in the canopy. Both species consumed a large proportion of fruit, but the spider monkeys spent a greater proportion of time feeding on fruit (87%) than did woolly monkeys (73%). The fruit chosen by spider monkeys included a significantly higher proportion of arillate capsular fruit and other lipid rich fruits in comparison with woolly monkeys. A similar study on sympatric lion-tailed macaques *Macaca silenus*, bonnet macaques (*M. radiata*) and Hanuman langurs (*Semnopithecus entellus*), found each primate species to forage at different heights in the forest and rely on different plant species or different plant parts and phenophases from shared plant parts (Singh et al. 2011). Similarly, a study of sympatric *Cercopithecus cambelli*, *C. petaurista*, and *C. diana*, found each species to forage at different heights of the forest and spend different proportions of time foraging on fruit and other dietary items (Buzzard 2006). These niche partitioning studies on primates provide important data on the organization and coexistence of primates in these communities. However, only a few of these studies have attempted to collect quantitative data on the interaction between primate species in the community (see Singh et al. 2011). Even the studies that provide quantitative data on species interaction, have failed to explore the consequences of these interactions on aspects of the ecology of primate species in the community. Hence, based on these studies, one can only hypothesize a casual link between ecological partitioning in primates and competition (Ganzhorn 1988).

1.2.6 Niche overlap and competition

Niche overlap has frequently been used as an indicator of the degree of resource partitioning and competition among organisms in a community (MacArthur and Levins 1967; Nakano et al. 1999; Bryce et al. 2002). Niche overlap refers to the utilization of some of the same resources by two or more species of same consumers (Abrams 1980). In spite of the general notion that there is some relationship between niche overlap and interspecific competition, there seems to be great ambiguity regarding the nature of this relationship and hence its suitability has met with criticism (Colwell and Futuyma 1971; Abrams 1980). Overlap may change in response to competition but knowing the amount of overlap in resources utilization between species indicates nothing about the intensity of competition (Abrams 1980). The intensity of competition depends on the ratio of consumer density to resource density and if all resources were halved in abundance, competition would generally become more intense, but overlap need not change (Abrams 1980). Also if resources are not in short supply, competition msy not occur even though there is overlap in resource use. Alternatively, if there is territoriality or if species actively alter their resource utilization to avoid a competitor, competition may occur in spite there being little or no overlap (Abrams 1980).

Although overlap may not be indicative of the intensity of competition, changes in overlap may better reflect the influence of interspecific competition (Korpimaki 1987). Competition theory predicts that the niches of species should vary spatially, as a function of distributions of closely related, potentially competing species, and temporally, as a function of variations in resource abundance and population densities of potential competitors (Llewellyn and Jenkins 1987). The spatial shift of niches in response to competition has been relatively well studied (Huey et al. 1974; Schoener 1975; Diamond 1978; Alatalo et al. 1985). These studies contrast niches of a species in the presence of potential competitors with niches when competitors are absent. Temporal shifts in niches in response to resource abundance have been observed in a large number of studies (Lack 1947; Smith et al. 1978; Lister 1980; Toft 1980; Korpimaki 1987; Holbrook and Schmitt 1989; Nakano et al. 1999).

Schoener (1982) in his review of studies on temporal niche shifts states that data on seasonal and year-to-year variability in ecological overlap are extremely important because of what they suggest about how competition operates in nature. If interspecific competition influences resource utilization, during lean times when species are likely to be in competition selection should act especially strongly to produce those sorts of specializations that result in niche separation (Schoener 1986). Hence in “lean” seasons during which resources are in short supply, resource utilization of ecologically similar species should diverge resulting in reduced niche overlap in comparison to “fat” seasons when resources become plentiful (Schoener 1982). The study by Zaret and Rand (1971) showed increased diet overlap between several species of fish in the wet season when food resources were abundant, and reduced overlap during the dry season when food was limited. An aggressive insectivorous surface feeder *Astyanax* displayed an entirely different foraging strategy by feeding in the middle region of the water body and consuming non insect food. This was due to the presence of another insectivorous surface feeder *Gephyrocharax sp*. In habitats where the species *Gephyrocharax* sp. was absent *Astyanax* sp. consumed a larger proportion of insects in relation to vegetative matter. Finches of the genus *Geospiza* diverged in their diets and took a narrower range of foods in the dry season when food became scarce (Smith et al. 1978). All species shifted from a common wet season diet of soft, easy to handle seeds and fruits to different diets reflecting the morphological specializations of each species. Also at two sites finch biomass declined as food supplies declined sharply.

Similar patterns of foraging microhabitat niche overlap have also been observed in some British birds (Lister 1980). A study of thirteen species of anurans revealed that within guilds similarity in diet was lowest in the dry season when food is less abundant (Toft 1980). Neighboring pairs of kestrels (*Falco tinnunculus*) and long-eared owls (*Asio otus*) with overlapping foraging areas, showed less diet overlap during years when vole densities were low than non-neighbors (Korpimaki 1987). Also neighboring pairs of both species produced fewer young than did non-neighboring birds. Two species of marine reef fishes, black surfperch (*Embiotoca jacksoni*) and striped surfperch (*E. lateralis*) when in shallow habitat, overlapped in preferred foraging microhabitat (red algae *Gelidium*) extensively during warm-water periods when prey was most abundant and declined during cold-water winter season when prey was less abundant (Holbrook and Schmitt 1989). The use of *Gelidium* substrate by striped surfperch declined from 80% in summer to 50% in winter. The reduced use of this substrate was associated with increased use of other substrates. The use of *Gelidium* substrate by black surfperch decreased from 40% in summer to 5% in winter. In winter the black surfperch narrowed its use of foraging microhabitats, concentrating mainly on turf alone. However when black surfperch was removed, striped surfperch increased its use of *Gelidium* substrate to >80% during winter. Similarly when striped surfperch was removed, black surfperch increased its use of *Gelidium* and decreased use of turf. Similar patterns have also been observed in two species of morphologically similar chars, *Salvelinus malma* and *S. leucomaenis* (Nakano et al. 1999). The two species showed high diet overlap and a high frequency of agonistic bouts when drift foraging. Agonistic bouts increase with decrease in drift levels, eventually causing a larger proportion of the subordinate species *Salvelinus malma* to shift to benthic foraging resulting in reduced diet overlap between the two species.

Similar patterns in resource overlap in relation to resource availability have also been observed in many primate communities. Three species of guenons, *Cercopithecus nictitans*, *C. pogonias*, and *C. cephus* overlapped extensively in diet during the major part of the year but declined during the dry season when fruit, young leaves and animal matter were in short supply (Gautier-Hion 1980). *Alouatta seniculus*, *Ateles paniscus* and *Aloutta seniculus* showed considerable diet overlap during periods of fruit abundance and reduced overlap and a more diverse diet during periods of fruit scarcity (Guillotin et al. 1994). Four species of primates *Sanguinus fuscicollis*, *S. mystax*, *Cebus apella* and *Lagothrix lagotricha* showed increased diet overlap during the wet season when fruit was abundant and reduced overlap during the dry season when fruit availability was low (Peres 1994). *Ateles belzebuth*, *Lagothrix lagothricha*, *Cebus apella* and *Aloutta seniculus* showed greater overlap during periods of fruit abundance and decreased during periods of fruit scarcity (Stevenson et al. 2000). Also a high degree of interspecific antagonistic bouts were observed during periods of increased diet overlap. *Lagothrix* *lagothricha* dominated the other species, exhibiting the most aggressive behaviors while receiving only a few (Stevenson et al. 2000). A similar pattern of diet overlap in relation to resource abundance was also observed in a primate community in the Lope Reserve (Tutin et al. 1997). In all of these studies the degree of niche overlap is more extensive during the period of resource abundance in comparison with the period of resource scarcity.

1.2.7 Competition in primates

Competition holds a central place in primate socioecology. Identifying the different factors that influence primate group size and social organization has been an important theme (Chapman et al. 1995; Steenbeek and van Schaik 2001). The most commonly cited tradeoff associated with group living is intragroup feeding competition which has been shown to cause increased mortality (Dittus 1979) and lower female reproductive rates (Whitten 1983). In addition, contest competition (Janson 1985; 1988) and scramble competition (Janson 1988; Chapman et al. 1995) have been shown to reduce foraging efficiency in primates. Exploitation competition has also been shown to affect primate group size when a group has to travel farther per day than a solitary forager does to satisfy energy requirements (Chapman et al. 1995; Janson and Goldsmith 1995). These predictions have lead to the formulation of the ecological constraints model of group size (Chapman et al. 1995; Chapman and Chapman 2000). This model is well supported by empirical data from frugivorous primates (Chapman et al.1995) and has been recently tested on colobines (Gillespie and Chapman 2001; Chapman and Chapman 2000).

As a result of their dietary specializations colobines are capable of ingesting large quantities of foliage and hence the group as a whole is often labeled as ‘the leaf eaters’. Hairston et al. (1960) suggested that herbivores do not compete partly because they are not food limited. Leaves have been identified as key food resource for colobines and since leaves are superabundant evenly dispersed, it is often assumed that within-group exploitation competition is weak or absent (Ripley 1970; McKenna 1979; Wrangham 1980; Steenbeek and van Schaik 2001). Since colobines and other folivores are free from within-group competition, theoretically they are free to form larger groups. But many folivorous primates including colobines live in relatively small groups (Rudran 1973a; Steenbeek and van Schaik 2001). This contradiction is referred to as the folivores paradox (Steenbeek and van Schaik 2001). Contrary to these predictions, several lines of evidence suggest that folivorous primates are food limited. A number of studies have shown that colobines are not mere obligate folivores and that they preferentially select high quality foods such as young leaves, fruit and seeds which are distributed in patches that are irregularly distributed in space and time (Oates 1994; Davies et al. 1999; Chapman et al. 2002). Also the availability of food, especially high quality foods has been shown to account for much of the variation in colobine biomass (McKey et al. 1981; Waterman et al. 1988; Chapman et al. 2002; Chapman et al. 2004). In addition, contest competition has also been documented in colobine monkeys (Koenig 2000; Koenig et al. 2004). Finally, Gillespie and Chapman (2001) in their test of the ecological constraints model on red colobus found that a larger group had longer day ranges than a smaller group and that the day range of the larger group increased further in response to decrease in food availability. These lines of evidence demonstrate that colobine monkeys are limited by food, and thus it is highly probable that they are susceptible to interspecific competition.

In addition to this evidence that colobine monkeys are susceptible to interspecific competition, a number of lines of evidence suggest that interspecific competition may be an important interaction in determining primate community structure. These lines of evidence include phenomena such as density compensation by medium-sized non-hunted primates such as *Pithecia* and *Cacajao* after the extinction of large-bodied primates such as *Alouatta*, *Lagothrix* and *Ateles* (Peres and Dolman 2000), positive correlation between ratios of body mass and the number of species at a site (Ganzhorn 1999), body size mediated dominance hierarchies in tropical frugivores (French and Smith 2005; Houle et al. 2010), aggressive interactions between species (Stevenson et al. 2000), and saturated primate communities (Lawes and Eeley 2000). Furthermore, a recent analysis of niche separation in primates demonstrated that the Asian region had the highest percentage of putative competitors in relation to other geographical regions (Schreier et al. 2009). The analysis of large and local scale patterns of primate diversity determined that diversity in Asian primate assemblages is saturated and that local diversity is probably influenced by strong local species interaction rather than regional diversity (Lawes and Eeley 2000).

Despite the evidence that points to the possible influence of interspecific competition on aspects of the ecology of primates, the broader role of interspecific competition in primate communities is unclear due to the paucity of studies addressing this topic (Stevenson et al. 2000; Tutin et al. 1997; Guillotin et al. 1994; Gautier-Hion 1980). The relatively few studies that have addressed this issue have predominantly focused on the relationship between diet overlap and resource availability to draw inferences regarding the influence of interspecific competition on primate dietary ecology. These studies have failed to carry out any other empirical tests to assess the impact of interspecific interaction on primate ecology (Tutin et al. 1997; Guillotin et al. 1994; Gautier-Hion 1980). In addition, the variation in dietary overlap in relation to food availability reported in these studies cannot be attributed to the action of interspecific competition alone because morphological and behavioral adaptations may also enable species to make dietary shifts similar to those caused by interspecific competition and exploit alternative types of foods as preferred food items become scarce (Korpimaki 1987; Marshall and Wrangham 2007).

1.3 The Colobinae

The Old World Monkeys (Africa and Asia) belong to one family, made up of two subfamiles, the Cercopithecinae and the Colobinae. The Colobinae get their name from the reduced or absent thumbs of the African species (Greek *Kolobos*, mutilated); Asian colobines have small thumbs (Oates and Davies 1994).

The most diagnostic feature of the colobines is their large multi-chambered stomach. The forestomach contains a rich anaerobic microbial fauna comprising of bacteria, protozoa and fungi (Kay and Davies 1994). The gastric contents are maintained at a pH ranging between 5.0 and 6.7, which permits an active fermentation of ingesta by the large number of anaerobic microbes present (Bauchop and Martucci 1968). Colobines premolars and molars are high crowned and possess pointed cusps linked by ridges and separated by deeper lateral notches (Oates and Davies 1994). The sharper crests and higher cusps fold and slice leafy food (Oates and Davies 1994). These dietary adaptations enable them to efficiently ingest and digest foliage.

Apart from their dietary specializations colobine monkeys are also an integral part of the ecosystem. In the Kibale Forest in Uganda the tree *Markhamia platycalyx* only produced fruit once in a 5-year period during which time *Markhamia platycalyx* flowered in synchrony to swamp red colobus predation. During other times red colobus were observed to remove all flowers from the trees. Struhsaker (1975) suggested that the synchrony in flowering is an adaptation that may have evolved in response to red colobus predation of flowers. In Sri Lanka, *Semnopithecus entellus* and *Trachypithecus vetulus* caused major changes to the floristic diversity in the study site after a cyclone depleted more than 50% of the woody vegetation (Dittus 1985). Preferentially browsed tree species that were relatively rare and/or small in size died at significantly greater rates due to overbrowsing in comparison to those that were buffered against over browsing by virtue of being large in tree size and/or relatively abundant in the forest (Dittus 1985).

1.3.1 Taxonomic status of Semnopithecus entellus and Trachypithecus vetulus

The true phylogeny of the extant colobines is uncertain. Based on distribution and morphology, the colobines are divided into an African and Asian clade (Oates et al. 1994). The Asian colobines, which are more diverse than African colobines, are further split into odd-nosed monkeys (*Rhinopithecus*, *Pygathrix*, *Nasalis*, *Simias*) and langurs (*Semnopithecus, Trachypithecus*, *Presbytis*) (Osterholz et al. 2008). Additional genera like Kasi are occationally used (Pocock 1939). Both, the odd-nosed monkey and the langur group are considered to be monophyletic (Osterholz et al. 2008). Most authors place the Hanuman langur in the genus *Semnopithecus* distinct from other langurs and leaf monkeys (Oates et al. 1994; Groves 2001). Hanuman langurs are one of the most wide distributed and morphologically variable species (Newton 1988). Studies examining the phylogenetic relationships between distinct populations based on mitochondrial and nuclear DNA, argue that Hanuman langurs should be split into three distinct species, the Northern type from North India, the Southern type from South India, and the Southern type from Sri Lanka (Osterholz et al. 2008; Karanth 2010). In the case of the purple-faced langur, some authors place the species in the genus *Trachypithecus* (Oates et al. 1994; Groves 2001), while others place it in the genus *Semnopithecus* (Brandon-Jones et al. 2004) or a distinct genus *Kasi* (Pocock 1939). However, recent work based on mitochondrial and DNA lends support to the taxonomy proposed by Brandon-Jones et al. (2004). To avoid any ambiguity, the classification proposed by Groves (2001) has been adopted in this dissertation.

1.3.2 Habitat and distribution of Semnopithecus entellus and Trachypithecus vetulus in Sri Lanka

Sri Lanka is a tropical island located off the southern tip of India. It is 65,000 km^2 in extent and has a human population of 18.7 million. The island is bordered on its east by the Bay of Bengal and the west by the Indian Ocean. The island has a remarkably varied topography, with coastal planes, lowland hills and a mountainous interior (Ashton et al. 1997). Sri Lanka’s equatorial position and its complex topography interact to produce distinct climatic zones: the dry zone (60% of the island), intermediate zone (15%) and the wet zone (25%). The complex topography and the diverse climates interact to produce distinct types of vegetation including rain forest, dry mixed evergreen forest, montane forest and shrub forest. The rain forest and the montane forest types are confined to the wet zone of the island and the dry mixed evergreen forest and the shrub forest types are confined to the dry zone of the island. Owing to its diverse climates and forest types, Sri Lanka is able to support a high level of biodiversity and hence, together with the Western Ghats of India, is considered to be a global biodiversity hotspot (Myers et al. 2000). Sri Lanka is home to four species of primates, the Toque monkey (*Macaca sinica*), the purple-faced langur (*Trachypithecus vetulus*), the grey langur (*Semnopithecus entellus*) and the slender loris (*Loris tardigradus*). The lorises are sometimes divided into multiple species distinct from the Indian forms (Brandon-Jones et al. 2004). Of these primates, the Toque macaque and the purple-faced langur are endemic to Sri Lanka (Phillips 1935), and so are the lorises pending further phylogenetic information.

In Sri Lanka, *Semnopithecus entellus* is represented by a much smaller subspecies *Semnopithecus entellus thersites* (Bennett and Davies 1994), which weighs between 6.8-13.4 kg (Phillips 1935). In Sri Lanka *Semnopithecus entellus* is found throughout the well-wooded areas of the whole dry zone from south of Jaffna, in the North, to the shores of the extreme southern coast (Phillips 1935) (Fig. 1.2). The purple-faced leaf monkey, *Trachypithecus vetulus* is endemic to Sri Lanka and is currently divided into four distinct subspecies, all occupying different geographic regions (Fig. 1.2). In contrast to the Hanuman langur, the purple-faced langur is predominantly confined to the wet zone of Sri Lanka. The four subspecies of *Trachypithecus vetulus* are distinguished based on pelage color and length, tail length and relative body size. On average *T. vetulus* weighs between 3.9 and 11.4 kg (Phillips 1935). The southern subspecies *Trachypithecus vetulus vetulus* is predominantly confined to the southern wet zone. *Trachypithecus vetulus* *nestor*, the western subspecies, is confined to the western and southwestern wet zone of Sri Lanka. The highland subspecies, *Trachypithecus vetulus monticola* is confined to the central hills and is found at altitudes ranging from 1150 m to 2300 m while the northern subspecies, *Trachypithecus vetulus philbricki* occupies north central, northwestern and northeastern dry zone (Phillips 1935). *Trachypithecus vetulus philbricki* is the only subspecies that shares its range with the grey langur, *Semnopithecus entellus*. *Trachypithecus vetulus philbricki* and *Semnopithecus entellus* are sympatric in the semi-evergreen forests of the central dry zone of Sri Lanka (Bennett and Davies 1994) (Fig. 1.1).

1.3.3 Ecology of Semnopithecus entellus and Trachypithecus vetulus

Semnopithecus entellus has a broad distribution and in addition to Sri Lanka is found throughout much of the Indian subcontinent from Pakistan through India and north through Nepal possibly into southern Tibet (Wolfheim 1983). In the mainland Indian peninsula, these monkeys inhabit diverse vegetation zones that include semi desert, open park woods, moist deciduous forests, and mountain forests (Koenig and Borries 2001). In Sri Lanka, the hanuman langur is predominantly confined to the dry zone from south of Jaffna, in the north, to the shores of the extreme southern coast (Phillips 1935).

The majority of the studies carried out on hanuman langurs have been done on populations inhabiting relatively disturbed habitats (Bishop et al. 1981; Newton 1988). Hanuman langurs exhibit social flexibility in relation to group size and the number of males per group in that they occur as multi-male and one-male bisexual groups (Newton 1988; Newton and Dunbar 1994). These two grouping patterns occur in varying frequencies throughout the Indian sub continent (Newton 1988). However, the one-male social unit is the predominant social unit in many study localities in India (see Table 1.1; Newton 1988; Koenig and Borries 2001). In a few study localities in northern Indian and in Sri Lanka, the multi-male social unit predominates (Ripley 1965; Boggess 1980; Borries 1997). The examination of this social variation and the ecological and behavioral processes that influence langur social structure have dominated the literature on hanuman langurs. In an analysis of 24 wild populations of hanuman langurs , Newton (1988) found that the number of adults was positively correlated with troop size and the number of adult females in the troop but failed to elucidate any relationship between the number of males in a group and the density of langurs, predation pressure, and economic-advantage hypotheses. In addition, reproductive synchrony and home range size (distance between groups) (Srivastava and Dunbar 1996), predatory pressure (Treves and Chapman 1996) and langur population density (Moore 1999) have also been shown to influence the number of males in a group. In the case of one-male groups, it is only the resident adult male that breeds (Sommer and Rajpurohit 1989). In multi-male groups, breeding is not entirely monopolized by the dominant male (Launhardt et al. 2001). In multi-male groups, the dominant male sired 57% of the infants in the group in one study (Launhardt et al. 2001). Resident male replacement and infanticide has also been reported in hanuman langurs (Sugiyama 1965; Mohnot 1971; Hrdy 1974; Newton 1986; Borries et al. 1999). In one-male groups that have been studied, residency of an adult male varied between 3 days and 74 months with a mean of 26 months (Sommer and Rajpurohit 1989). However, the tenure of adult males in multi-male groups changes less drastically (Laws and Vonder Haar Laws 1984). Juvenile males emigrate from their natal troops and often join together to form all-male bands (Reena and Ram 1991). Males living outside their natal troops suffer high levels of mortality in comparison to philopatric females (Rajpurohit et al. 1995). The transfer of females between groups has also been recorded (Newton 1987).

Hanuman langur females establish dominance hierarchies that are age-inverse (Hrdy and Hrdy 1976; Borries et al. 1991). The body condition of adult females is correlated with dominance rank, with high-ranking females being in best condition (Koenig 2000). However, ranks are unstable and are often difficult to establish for forest dwelling populations (Ripley 1965; Newton and Dunbar 1994). Adult male hanuman langurs tend to remain aloof from troop activities and are reported to be mainly responsible for intertroop spacing (Ripley 1965). Troop spacing is maintained through whooping vocalizations elicited by adult males (Ripley 1965). Hanuman langurs are predominantly seasonal breeders with mating occurring during the monsoon season (Sommer and Rajpurohit 1989; Borries et al. 2001) and most births occurring during dry season from December to June (Newton 1987; Newton and Dunbar 1994). Female hanuman langurs have a mean cycle length of 24 days and a mean gestation period of 200 days (Sommer at al. 1992). These life history traits are influenced by the nutritional condition of females (Borries et al. 2001).

Hanuman langurs maintain home ranges ranging from 0.80 km^2 to 6.60 km^2 and occur in densities ranging from 2 animals per km^2 to 112 animals per km^2 (Srivastava and Dunbar 1996). In Sri Lanka, the core area of *Semnopithecus entellus* constitutes a greater proportion of the home range in comparison to *Semnopithecus entellus* in India (Ripley

1967). Although categorized as folivorous, hanuman langurs are eclectic feeders and consume a diverse array of plant species (Ripley 1970; Newton 1992). The feeding rate on seasonal food items has been shown to be higher than when feeding on perennial food items (Ripley 1970). Contest competition in the context of feeding has been reported for hanuman langurs (Koenig 2000; Koenig et al. 2004). In contrast, competitive interactions have been rarely observed in other populations (Ripley 1970). In Polonnaruwa, interaction during feeding is kept to a minimum by the body orientation adopted by individual animals and by the vegetation acting as a natural barrier between animals (Ripley 1970). Grey langurs are capable of surviving without a source of surface water for several months at a time (Ripley 1965; 1967).

Much of what is known about the ecology of *T. vetulus* in Sri Lanka is largely from studies carried out at Polonnaruwa, a heavily disturbed secondary dry zone forest where considerable provisioning of primates occur. Only the study by Rudran (1973a; 1973b) was carried out in an undisturbed habitat in Sri Lanka. Rudran (1973a; 1973b) studied the ecology of *T. vetulus monticola* in an undisturbed montane forest at Horton Plains in the highlands and *T. vetulus philbricki* at Polonnaruwa. For both subspecies, the one-male troop is the predominant troop structure, which remains stable for relatively long periods of time (Rudran 1973a). The population density, home range and group size of *T. vetulus* differ at the two study sites (Table 1.3). Changes in composition of one-male troops occur mainly due to births and to the deaths of infants and juveniles. In addition to the one-male groups, predominantly-male troops have also been observed. The age classes of the males that constitute the predominantly-male troops range from adult to juvenile, while while the infrequent females that belong to these groups fall in the immature age classes only.

Adult male replacement has been observed in the Polonnaruwa population (Rudran 1973a). However, adult male replacement has not been observed in langurs inhabiting the montane forests of Sri Lanka (Rudran 1973b). During adult male replacement of a group, all immature individuals of the group are gradually expelled from the group (Rudran 1973a). A high degree of antagonistic behavior was observed between one-male groups and extra-troop males. Also, a greater number of one-male troops at Horton Plains included juveniles and subadults. Rudran (1973a) attributed adult replacement as the major cause for high infant mortality, small percentage of immature individuals and lack of graded age class structure in the majority of the one-male troops at Polonnaruwa.

T. vetulus monticola and *T. vetulus philbricki* differ in their reproductive cycles (Table 1.3). At Polonnaruwa, the mating peak and early phase of gestation coincides with the period of rainfall, abundant food supply, decreasing temperature and day length (Rudran 1973b). Infants born during this birth peak are old enough to exploit solid food items during the following period of food abundance (Rudran 1973b). Synchronization of births was also caused by adult male replacements in one-male troops, regardless of the time of occurrence of such social changes. At Horton Plains, where rainfall and food availability remain relatively high throughout the year and environmental correlates of the reproductive cycle of *T. vetulus monticola* are not easily recognizable (Rudran 1973b).

The hanuman langur and the purple-faced langur (*Trachypithecus vetulus*) overlap in their ranges in the north central dry zone of Sri Lanka (Bennett and Davies 1994). When sympatric, the two species have been reported in one study to partition food according to type (Hladik 1977). At Polonnaruwa, where both species occur, *T. vetulus* maintain small territories of about 2-3 ha and obtain food from the most common species. In contrast, *S. entellus* occupy territories of 10 to 15 ha, are less arboreal and utilize a more diverse array of plants than *T. vetulus*. During February and March *T. vetulus* feed on a high proportion of leaves (95%) including a high proportion of leaves and shoots than *S. entellus*. *Semnopithecus entellus* also include a high proportion of shoots and leaves during this time. In the dry season (May-June), the amount of leaves in the diet of both species decrease as fruits became more available. However *S. entellus* included more fruit in its diet in comparison to *T. vetulus*. During the major dry season large amounts of flowers are consumed by *T. vetulus* while *S. entellus* still included many fruits in its diet. During October and November, both species included shoots and young leaves and shoots in their diet but *T. vetulus* utilizes a lesser amount mixed with mature leaves in comparison to *S. entellus*. During December to January, leaves increase in the diet of both *S. entellus* and *T. vetulus* as shoots become less available. Although the diet of *S. entellus* and *T. vetulus* consists of different proportions of types of food items, the two species shared many food tree species raising the possibility for interspecific competition. The diets of *T. vetulus* and *S. entellus* at Polonnaruwa are given in Table 1.4

Ripley (1965) suggested that the apparent tolerance shown by hanuman lagurs for the lack of surface drinking water has enabled it to colonize areas that are outside the limits of tolerance of *P. vetulus* in Sri Lanka. Since hanuman langurs inhabit the extremely wet regions of India (Jay 1965; Singh et al. 1997), Ripley (1965) stated that the presence of *T. vetulus* in the wet zone of Sri Lanka has prevented the hanuman langur from colonizing the wet zone forests of Sri Lanka. In Polonnaruwa, hanuman langurs and purple-faced langurs avoided each other in areas where their home ranges overlap. On one occasion, a purple-faced langur ran along the ground in the direction of a hanuman langur group and managed to disperse the group. Based on these anecdotal observations and the distribution of the two species, Ripley (1965) suggested that competitive interactions occur between the hanuman langur and purple-faced langur and that the hanuman langur is subordinate to the purple-faced langur.

1.4 Statistical analyses

Primate behavioral data have been shown to be non-normally distributed, with variances that are typically heterogeneous (Agostini et al. 2010). Hence, non-parametric statistical procedures were adopted to analyze data presented in this dissertation. While non-parametric tests have lower power when compared to parametric statistics under conditions in which the distributions conform to parametric assumptions, they remain valid for inferential testing when the parameters of parametric statistics are violated, and thus are the appropriate choice. Non-parametric tests do assume that observations are all independent. This is a very difficult assumption to meet in most data sets of free-ranging primate behavior. Observations are often linked because they are sampled in time sequences, from the same individual, from the same habitat patch, or other common variables. These cannot be controlled in the field. In cases when lack of independence of individual data points may impact statistical testing, this will be noted.

The habituation of primate groups to human observers is often time consuming and consequently only a few groups can be successfully habituated during the course of a field study. Hence, primatologists are often compelled to confine their data collection to habituated groups, which are few in number (Hladik 1977; Gautier-Hion 1980; Dew

2005). Most behavioral data sampling methodologies employed by primatologists involve recording the current behavior of an individual or group of individuals at predetermined time intervals (Chapman et al. 1995; Buzzard 2006). These methods involve the sequential observation of a few individuals and hence the data points are interdependent but the extent to which this impacts any given behavioral data remains unknown. In addition, other assumptions of random sampling are also violated as sampling is frequently focused on a few individuals often chosen because of convenience rather than by a random process (Dagosto 1994). Thus, the application of standard parametric and non-parametric tests, which assume data independence to primate behavioral data, is problematic. However, arguments have also been made that sequential events are independent enough for the application of some types of statistical techniques as the same behavioral event is often not observed twice and only requirement necessary for two events to be independent is that subsequent action is not influenced by the previous choice (Bakeman and Gottman 1986; Dagosto 1994). This assumption is surely violated, but the frequency or importance of the violation is unknown.

A number of statistical procedures such resampling and randomization have been adopted by investigators to minimize the influence of interdependence of behavioral data on statistical inference (Dagosto 1994; Rehg 2006). In some forms, resampling methods select data points at random from larger sets to break down the autocorrelation of time sequences. Other resampling strategies may help break down the interdependence on observations of individual monkeys. In all cases, re-sampling of primatological data cannot generate data sets that are known to be free of all problems of interdependence. (Potvin and Roff 1993; Dagosto 1994). Behavioral data collection in this study was carried out using group scan sampling (Altmann 1974). Scan sampling was carried out at a longer 10 minute intervals to improve the chances that a behavior observed during a particular scan was not influenced by the behavior observed in the previous scan. However, the data presented here have not been randomized or resampled, and hence, the statistics presented here should be interpreted with the caveat that they may have been influenced by data interdependence. This means that sample size is artificially inflated in many cases, and therefore the degrees of freedom and the alpha levels are to be interpreted accordingly, with reported results probably being biased in favor of a significant result rather than the other way around.

1.5 Organization of the thesis

In this dissertation new data on the ecology and behavior of sympatric groups of Hanuman and purple-faced langurs are presented with the view of addressing the question of whether interspecific interactions influence the feeding, habitat and ranging patterns of these foli-frugivorous primate species and also broadening the understanding of the ecology of these species and colobines in general. In the first chapter, I provide an overview of interspecific competition in primate and ecological communities in general and a theoretical framework for presenting and analyzing data presented in the subsequent chapters. Each subsequent chapter contains an introduction, a short description of the study area, methods, results and discussion section. In Chapter 2, I compare the vegetation, rainfall, and population status of the two primate species at the study site, to vegetation and population status of colobine monkeys at other study localities. I also compare the performance of population survey methods frequently used by primatologists. In Chapter 3, I describe aspects of the feeding ecology of the two primate species with the view of determining whether the patterns of resource use by these primates and the spatial distribution of resources can elicit interspecific interactions in these primate species. In Chapter 4, I present data on ranging behavior of the two study species. In this chapter, I specifically investigate aspects such as home range overlap, daily path length and intensity of home range use with intention of identifying aspects of ranging behavior that facilitate interspecies interactions and coexistence. In addition, I also explore the relationship between group size and monthly resource availability on aspects of ranging behavior. In Chapter 5, I explore the relationship between the monthly dietary overlap and monthly food availability and the consequences of interspecific interaction on foraging effort and the vertical habitat use patterns of these primates. The specific predictions outlined in Chapter 1 are also addressed in Chapter 5. In Chapter 6, I summarize the results of the previous chapters and evaluate whether interspecific competition influences aspects of the ecology of these primate species.

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1.7 Tables

Table 1.1. Average group size and the frequency of occurrence of the different group structures of hanuman langurs at different study localities throughout the Indian subcontinent

Location	AVTS	AVBS	%OMG	%MMG
Jodhpur Rajastan, India[1]	32	19	64	5
Dharwar Karnataka, India[2]	15	12	63	23
Jaipur Rajastan, India[3]	50	22.9	66	8
Aravali Hills Rajastan, India[4]	42	16	69	0
Madhav national park, India[5]	21	8	64	7
Kanha tiger reserve, India[6]	22	15	71	4
Anaimalai Hills, India[7]	19*	-	-	-
Nagarahole, Bandipur, Mudumalai, India[8]	18.6	7.8	85**	
Nadia district, West Bengal[9]	22	6	67	0
Abu[10, 11]	21	-	87.5	12.5
Orcha[12]	19	1	0	100
Kaukori[12]	54	3	-	100
Keshabpur-Manirapur, Bangladesh[13]	15.8	-	40	60
Ramnagar, Nepal[14]	16.9	-	23.5	76.5
Polonnaruwa[15, 11]	24	-	27	73

AVTS, average troop size; AVBS, average band size; OMG, one male groups; MMG, multi male groups; -, no data available; *, source only provides information on group size but does not specify if groups counted are all bisexual troops or include all-male bands; **, source provides details on only the % of bisexual groups. Sources: (1) Mohnot (1984); (2) Sugiyama and Parthasarathy (1978); (3) Mathur and Ram (1993); (4) Chhangani and Mohnot (2003); (5) Kankane (1984); (6) Newton (1987); (7) Singh et al. (1997); (8) Vasudev et al. (2008); (9) Das-Chaudhuri and Roy (1988); (10) Hrdy (1977); (11) Newton (1988); (12) Jay (1965); (13) Khan (1984); (14) Borries (1997); (15) Ripley (1965).

Table 1.2. Diet of *S. entellus* at four study localities in South Asia.

	Fruit (%)	Flowers (%)	Leaves (%)	Seeds (%)	Insects (%)
Kanha [1]	24.5	9.5	51.6	-	2.8
Ramnagar[2]	20.0	7.8	57.7	-	2.4
Rajaji[3]	12.9	17.9	56.6	12	-
Polonnaruwa[4]	45	7	48	-	-

Sources: (1) Newton (1992); (2) Koenig and Borries (2001); (3) Kar-Gupta and Kumar (1994); (4) Hladik (1977).

Table 1.3. A comparison of the populations of *T. vetulus* in Polonnaruwa and Horton Plains (based on Rudran 1973a; 1973b).

	Polonnaruwa	Horton Plains
Population density	215 km^{-2}	92.6 km^{-2}
Average group size	8.4	8.9
Home range size	2.5 ha	6.8 ha
Birth seasonality	May-August	Not found
Interbirth interval	22-25 months	16-17 months

Table 1.4. A comparison of the diet of *S. entellus* and *T. vetulus* in Polonnaruwa.

	Fruit (%)	Flowers (%)	Leaves (%)
S.entellus	45	7	48
T.vetulus	28	12	60

Figures 1.8

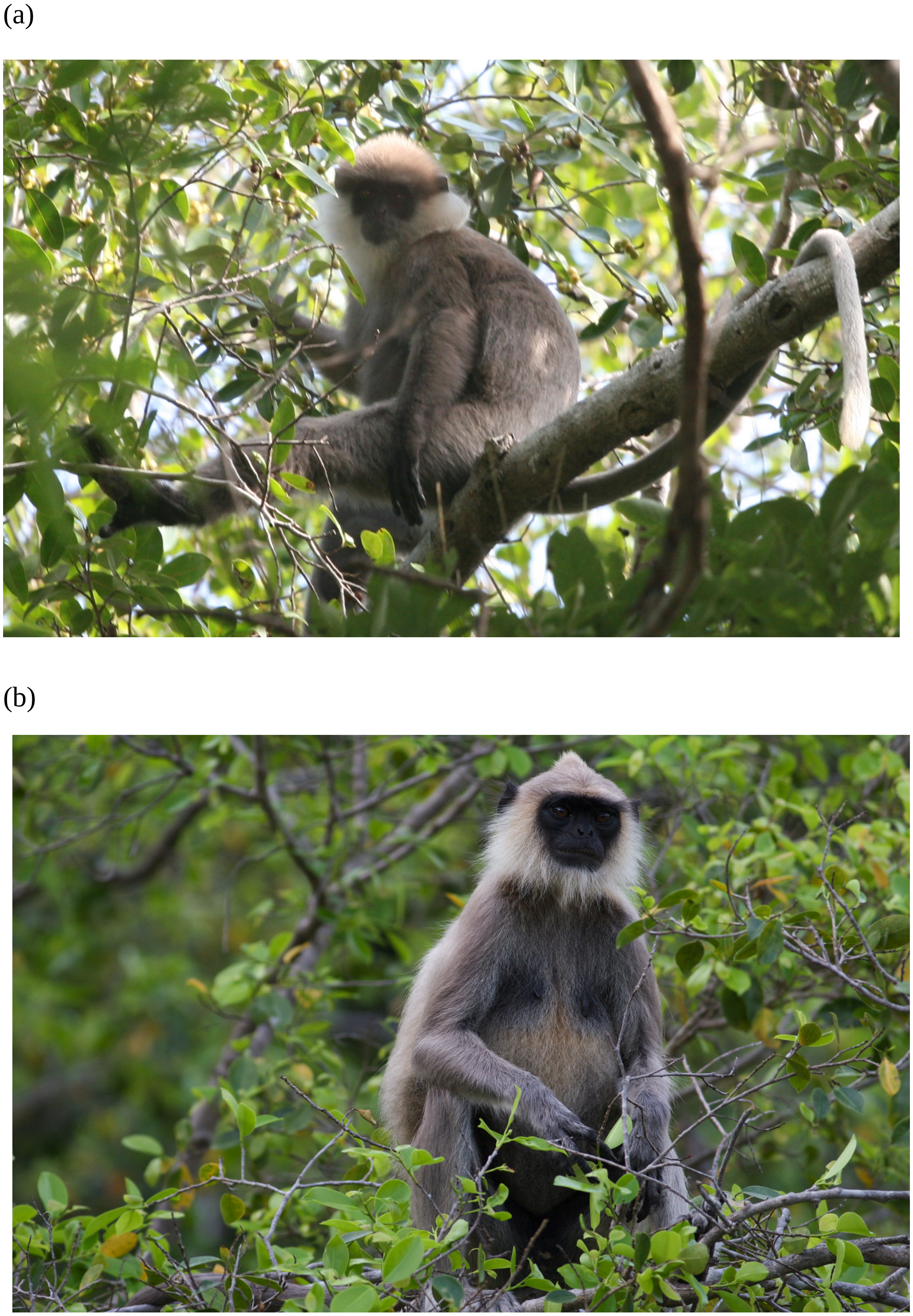

Figure 1.1. (a) *Trachypithecus vetulus philbricki* and (b) *Semnopithecus entellus thersites*

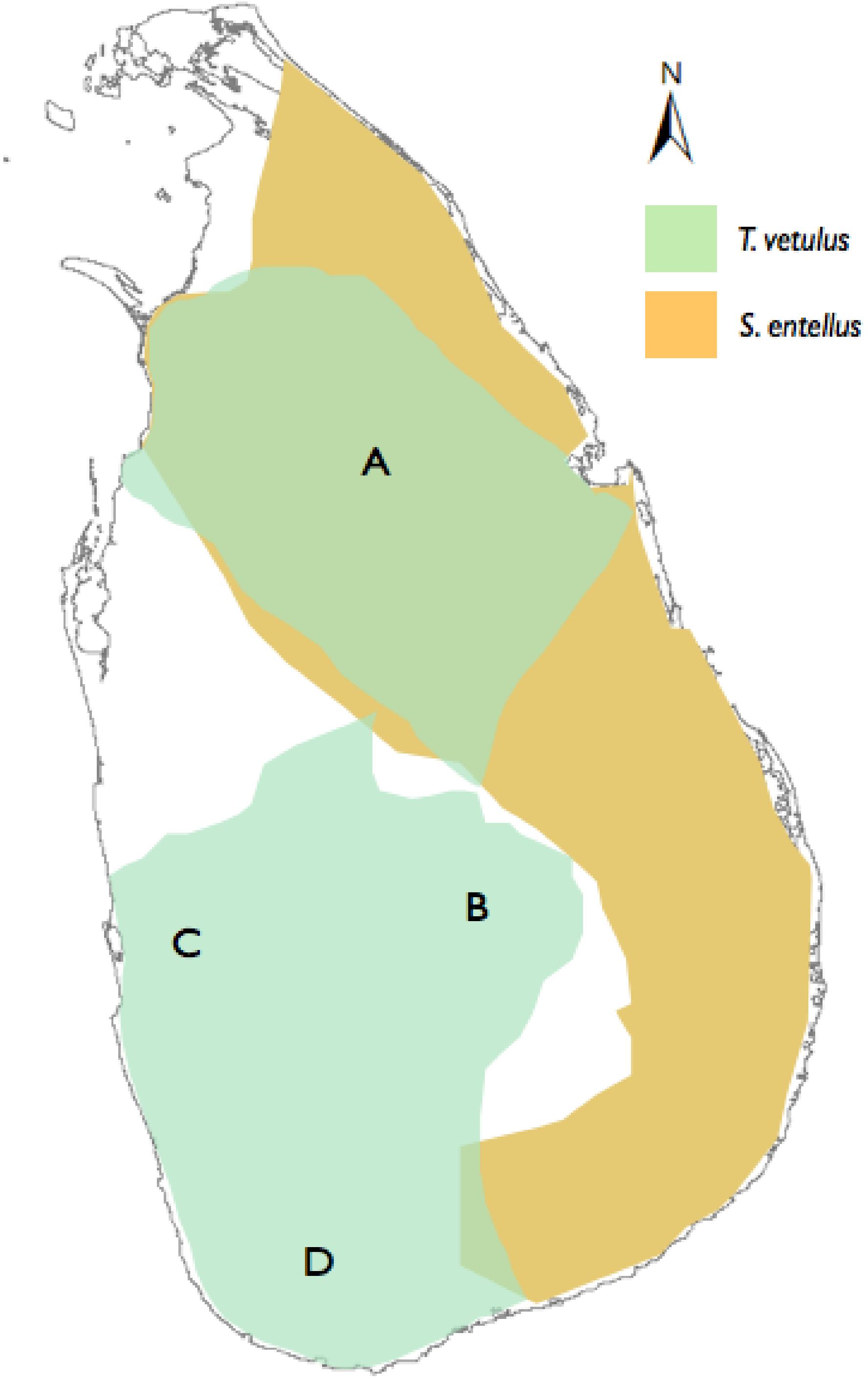

Figure 1.2. The approximate geographical distributions of *S. entellus thitsites* and the four subspecies of *T. vetulus* in Sri Lanka based on descriptions by Phillips (1935). A= *T. vetulus philbricki*; B= *T. vetulus monticola*; C= *T. vetulus nestor*; D= *T. vetulus vetulus*.

Chapter 2

Habitat description and the status of *Trachypithecus vetulus* and *Semnopithecus entellus* at the Kaludiyapokuna forest reserve, a long-term primate study site in the dry zone of Sri Lanka

2.1 Introduction

Sri Lanka is a tropical island located off the southern tip of India. It is 65 000 km^2 in extent and has a population of 18.7 million. The island is bordered on its east by the Bay of Bengal and the west by the Indian Ocean. The island has a remarkably varied topography, with coastal plains, lowland hills and a mountainous interior (Ashton et al. 1997). Sri Lanka’s equatorial position and its complex topography interact to produce distinct climatic zones: the dry zone (60% of the island), intermediate zone (15%) and the wet zone (25%). The complex topography and the diverse climates interact to produce characteristic types of vegetation including rain forest, dry mixed evergreen forest, montane forest, and shrub forest. The rain forest and the montane forest types are confined to the wet zone of the island and the dry mixed evergreen forest and the shrub forest types are confined to the dry zone of the island. Owing to its diverse climates and forest types, Sri Lanka is able to support a high level of biodiversity and hence, together with Western Ghats of India, is considered to be a global biodiversity hotspot (Myers et al. 2000). Based on the classification proposed by Brandon-Jones et al. (2004), Sri Lanka is home to three species of catarrhines, the Toque monkey (*Macaca sinica*), the purple-faced langur (*Trachypithecus vetulus*), the grey langur (*Semnopithecus entellus*) and two or more species of slender loris (*Loris* spp.). Of the diurnal primates, *Macaca sinica* and

Trachypithecus vetulus are endemic to Sri Lanka (Phillips 1935; Brandon-Jones et al. 2004).

The purple-faced langur (*Trachypithecus vetulus*) and the grey langur (*Semnopithecus entellus*) are two species of colobines that inhabit the island of Sri Lanka. *Semnopithecus entellus* has a broad distribution and in addition to Sri Lanka is found throughout much of the Indian subcontinent from Pakistan through India and north through Nepal possibly into southern Tibet (Wolfheim 1983). In Sri Lanka, *Semnopithecus entellus* is represented by a physically much smaller subspecies, *Semnopithecus entellus thersites* (Bennett and Oates 1994). In Sri Lanka *Semnopithecus entellus* is found throughout the well-wooded areas of the entire dry zone from south of Jaffna, in the North, to the shores of the extreme southern coast (Phillips 1935). The purple-faced leaf monkey, *Trachypithecus vetulus*, is endemic to Sri Lanka and is divided into four distinct subspecies, each occupying different geographic regions. The four subspecies of *Trachypithecus vetulus* are distinguished based on pelage colour and length, tail length and relative body size. The southern subspecies *Trachypithecus vetulus vetulus* is predominantly confined to the southern wet zone. *Trachypithecus vetulus nestor*, the western subspecies, is confined to the western and southwestern wet zones of Sri Lanka. The highland subspecies, *Trachypithecus vetulus monticola* is confined to the central hills and is found at altitudes ranging from 1150 m to 2300 m, while the northern subspecies, *Trachypithecus vetulus philbricki* occupies north central, northwestern and northeastern dry zones (Phillips 1935). *Trachypithecus vetulus philbricki* is the only subspecies that shares its range with the grey langur, *Semnopithecus entellus*. *Trachypithecus vetulus philbricki* and

Semnopithecus entellus are sympatric in the semi-evergreen forests of the central dry zone of Sri Lanka (Bennett and Oates 1994).

The most extensive type of vegetation in Sri Lanka is the dry mixed semi-evergreen forest, which is found throughout the dry zone of Sri Lanka (Ashton et al. 1997). These forests are of strategic importance to the conservation of Sri Lanka's primates as they support populations of all three of Sri Lanka's diurnal primate species, *Macaca sinica*, *S. entellus,* and *T. vetulus* (Phillips 1935). These forests are also of importance to the populations living in the rural areas in the dry zone as people depend on the forests for food, medicine and construction material (Perera 2001). Although these forests are the most extensive forest type in the island, they are fast disappearing as a result of infrastructure development initiated by the government, population growth in rural areas and the ensuing expansion of agriculture (Perera 2001). Sri Lanka has one of the highest rates of deforestation in the Asian region (Dinerstein and Wikramanayake 1993) and is the global biodiversity hotspot that has the highest category of population pressure (Cincotta et al. 2000). As a result of rapid deforestation, the long-term survival of Sri Lanka's primates is under threat (IUCN 2011).

Much of what is known about the ecology of *S. entellus* (Ripley 1965; 1967; 1970) and *T. vetulus philbricki* (Hladik 1977) in Sri Lanka is from studies carried out at Polonnaruwa sanctuary, a secondary semi-evergreen dry zone forest in the north central region and more recently from a study on *T. vetulus nestor* in home gardens and rubber plantations in the western region of Sri Lanka (Dela 2007). Only the study by Rudran (1973a; 1973b) on *T. vetulus monticola* was carried out in an undisturbed habitat in Sri Lanka. A few studies on a primate population at a single locality at one point in time may not be adequate to understand the flexibility of the ecology of these species. A study on *Procolobus tephrosceles* at six localities in and around Kibale National Park found significant differences in the ecology of animals among sites (Chapman and Chapman 1999). Similar observations have also been made in the case of *Procolobus badius* in and around Kibale National Park (Chapman et al. 2002). The differences in the ecology of the same species inhabiting different localities within a relatively small geographic area can be largely attributed to differences in the plant communities among these sites (Chapman and Chapman 1999). Hence, the findings of a few studies carried out at a particular location cannot be generalized to species characteristics, and this is presumably true also for *T. vetulus* and *S. entellus*, which have broad geographic distributions in Sri Lanka.

The Polonnaruwa sanctuary encompasses religious shrines and archaeological sites and hence is visited by large numbers of local and foreign tourists, who along with local residents use sections of the sanctuary as open toilets, for recreation, and for the disposal of food refuse (Ekanayake et al. 2006). In addition, local farmers graze their cattle in the Polonnaruwa sanctuary (Ekanayake et al. 2006). Hence, the Polonnaruwa study site is heavily disturbed and the disposal of food refuse within the sanctuary could be considered a form of provisioning of primates within the study area. Provisioning has been shown to alter ecological aspects such as activity budgets, home range size, and daily path lengths, as well as socio-biological aspects such as dominance hierarchies in primates (Altmann and Muruthi 1988; Borries at al. 1991). Thus, studies based on provisioned or populations living in disturbed habitats cannot be generalized to populations of primates living in undisturbed forest habitats.

A number of studies on wild primate populations have revealed a high degree of intersite variability in biomass (Oates et al. 1990; Ganzhorn 1992; Kay et al. 1997) and that food availability plays a key role in determining primate biomass and diversity (Kay et al. 1997; Stevenson 2001; Brugiere et al. 2002). Thus, comparing and contrasting floral diversity and structure between study sites is essential in interpreting differences in the behavior and abundance of primates between sites. In 2005, a long term study of the comparative ecology of sympatric populations *S. entellus* and *T. vetulus* was initiated in a relatively undisturbed location, the Kaludiyapokuna forest reserve, in the north central dry zone of Sri Lanka. This chapter compares the vegetation diversity and the status of the populations of *T. vetulus* and *S. entellus* at Kaludiyapokuna and Polonnaruwa, and discusses factors that influence the local abundance of primates, especially colobine monkeys. This chapter also examines the appropriateness of the frequently used rapid survey techniques for the estimation of primate group size by comparing the group size estimates for the two species obtained using rapid survey techniques and from total counts of fully and partially habituated groups. In addition, threats and challenges to the long-term survival of these primates in Sri Lanka are discussed.

2.2 Material and methods

2.2.1 Study site

The study was conducted in the Kaludiyapokuna forest reserve (N 07° 52.5, E 080° 44.1) located in the Matale district in the north central dry zone of Sri Lanka (Fig. 2.1). The study was conducted under the authority of the Department of Wildlife Conservation of Sri Lanka and in collaboration with the University of Peradeniya, Sri Lanka. The main study area is approximately 2.2 km^2 in extent and is contiguous with the Knuckles forest range in the south. The study site is surrounded by farmland and human settlements on the north, east, and west, and is unique because unlike the Polonnaruwa study site, which is disturbed and where primates have become accustomed to humans through regular contact (Bishop et al. 1981), this site is undisturbed by humans and the primates are not provisioned. There is neither evidence to indicate that hunting, timber extraction nor woodcutting took place at the site. The study site supports populations of four of the five species of primates of Sri Lanka. Apart from primates, the study site supports populations of other herbivorous mammals such as Asian elephants (*Elephas maximus*), spotted deer (*Axis axis*), sambar deer (*Cervus unicolor*), and wild pig (*Sus scrofa*). Unlike Polonnaruwa (Bishop et al. 1981), this study area is home to a full complement of potential primate predators such as the black eagle (*Ictinaetus malayensis*), leopard (*Panthera pardus*) and python (*Python molurus*).

The study area receives about 1250 mm of rainfall annually (Fig. 2.2) and average temperature in the region ranges between 27-29 º C. The region receives most of its rainfall through convectional rains from October to November, which gradually grade into the northeast (NE) monsoon. The NE monsoon lasts from December to February and is most active during the month of December. The NE monsoon brings considerably less moisture than the southwestern (SW) monsoon, which lasts May to September. The northern dry zone is shielded from the SW monsoon rains by the central hills of the island and hence experiences a characteristic period of drought during this time.

2.2.2 Characterization of vegetation

Vegetation sampling was carried out using vegetation plots (Ganzhorn 2003). This method was chosen because of the relative ease with which plots can be set up and sampled. Localities for sampling were chosen with the aid of a WorldView 1 satellite image of the study area and care was taken to ensure that the localities were evenly distributed across the study area so that an unbiased representative sample of the vegetation could be obtained. Each plot was 20 x 20 m in extent and 59 plots were used to sample the vegetation at the study site. The trees that were greater than 9 cm in diameter at breast height (DBH) and liana species were measured using a DBH tape and recorded. To sample understory vegetation, 15 of the sampling plots were further divided into two smaller 10 m x 20 m sub-plots, and the understory species within the sub-plots were counted and recorded. During sampling, a species area curve was constructed for tree species to determine the adequacy of the sampling effort (Fig. 2.3). Plant samples were collected and herbarium sheets were prepared and the specimens were identified and compared to voucher specimens at the National Herbarium at the Royal Botanical Gardens, Peradeniya, Sri Lanka. The importance value index (IVI) was calculated for each species (Curtis and McIntosh 1951). The IVI incorporates, relative density, relative frequency and relative dominance into one measure or index. Relative dominance of a given species was calculated as the total basal area of the species as a proportion of the basal area of all trees included in the sampling plots. The IVI is desirable since it gives prominence to species that tend towards large size and are abundant over those that are not (Dittus 1977).

The spatial distribution of tree species was also assessed using the Morisita Index of Dispersion (I_d) and Standardized Morisita Index (I_p) (Krebs 1999). Morisita's index (I_d) assumes unity (1.0) for a random distribution, over 1.0 for a clumped distribution, and less than 1.0 for a uniform distribution. The Standardized Morisita Index (I_p) ranges from -1.0 to + 1.0, with 95% confidence intervals at ± 0.5. Random patterns give a value of zero, clumped patterns above zero and uniform patterns below zero. The null hypothesis of randomness was tested by computing a χ^2 statistic for index values (Krebs 1999).

2.2.3 Population density estimation

An initial census was carried out in 2005 during the preliminary survey of the study site. In this census, the Recce transect method was used to estimate the relative abundance of *T. vetulus* and *S. entellus* (Sussman and Phillips-Conroy 1995; Walsh and White 1999). The natural trails within the study area were traversed during the morning and at dusk, and the number of animals encountered along these paths was recorded. A total of 21.6 km of trail within the study area (2.2 km^2) was traversed during the initial phase of the study. Efforts were made to record the morphological deformities and other external identification markers of animals encountered to avoid recounting the same troop (Struhsaker 1975).

A second census was performed during the course of January 2008 and June 2009, when groups were being habituated and behavioral and ecological data on both species were being collected. During this period most groups were semi or fully habituated and hence direct counting of individuals in the groups within the study area was possible. When groups were encountered, morphological deformities and other external identification markers of animals were recorded to avoid recounting the same troops. When possible, the age and sex composition of the groups were recorded. The density of langurs was determined by dividing the total animals encountered by the extent of the main study area.

2.3 Results

2.3.1 The number of tree species

A total of 2110 trees were encountered in the 59 plots that were used to characterize the vegetation at the Kaludiyapokuna forest reserve. The total number of tree species found was 73, belonging to 58 genera and 30 families. The species, their densities, relative densities, relative basal areas and IVI are tabulated in Table 2.1. The table also contains species that were found within the study area, but not included in the sampling plots because of either being too rare, as in the case of *Suregada angustifolia*, or those which occurred under certain edaphic conditions as in the case of *Memocylon sylvaticum*, which grew on rocky outcrops with thin soil layers. These rocky outcrops were difficult to access and hence the vegetation that grew in such localities was not systematically sampled.

Based on importance, the tree community was largely dominated by species belonging to the families Euphorbiaceae, Sapindaceae and Ebenaceae (Table 2.1). This was achieved largely due to the tree species such as *Mischodon zeylanicus*, *Drypetes sepiaria*, *Mallotus eriocarpus*, *Dimorphocalyx glabellus*, of the family Euphorbiaceae, *Diospyros oocarpa* and *D. ovalifolia* of the family Ebenaceae, and *Lepisanthes senegalensis* of the family Sapindaceae, which were abundant throughout the study site. The importance value index (IVI) is a measure that incorporates relative density, relative frequency, and relative basal area into one index and hence is a better estimate of the relative importance of a particular plant species to a plant community than any one measure alone. Thus, species that were abundant and small in trunk size ranked highly in relation to relative density but ranked lower in relative importance, while some species which ranked lower in relation to relative density ranked higher in relative importance by virtue of large trunk size (Table 2.2). The gains in rank were particularly evident in species such as *Holoptelea integrifolia*, *Ficus microcarpa* and *Ficus amplissima* which were large trees with buttresses, which may have resulted in a slight exaggeration of trunk size in these species (Table 2.2).

The canopy was largely composed of species such as *Mischodon zeylanicus*, *Diospyros oocarpa, Pterospermum suberifolium*, *Dimocarpus longan* and *Lepisanthes senegalensis*. Species such as *Drypetes sepiaria, Allophylus serratus*, *Cryptocarya* sp., *Mallotus philippensis,* and *Grewia rothii* constituted a subcanopy layer. *Tetramales nudiflora* and *Holoptelea integrifolia* were large trees that were 30-40 m in height and constituted an emergent layer.

2.3.2 The abundance of trees according to size classes

The DBH measurements of 1139 trees from 44 plots was analyzed to characterize the size distribution of trees at Kaludiyapokuna. The DBH of trees at Kaludiyapokuna ranged from 9 cm to 275.2 cm with a mean and mode of 24.4 cm (SD ± 23.61) and 9 cm respectively. The examination of the data showed that most trees were small in diameter and the number of trees decreased rapidly with the increase in trunk diameter (Fig. 2. 4). In addition, most species were also small in trunk diameter and the number of tree species declined rapidly with increase in trunk diameter (Fig. 2.5). Small stems (9-29 cm DBH) contributed to approximately 80% of total species richness.

2.3.3 Spatial distribution of tree species

Spatial patterns were computed only for species that were encountered in sufficiently large numbers in the sampling plots (Table 2.3). Most tree species were clumped in their distribution. Three species, *Ficus microcarpa*, *Dialium ovoideum* and *Wrightia angustifolia*, were randomly distributed.

2.3.4 Lianas and understory species

The total number of liana and climber species was14, belonging to 14 genera and 13 families. A climber was considered to be a plant with stems that had little or no ability to bear weight and utilized other plants or rocks for support. A liana was considered to be a woody climber with roots on the forest floor but with leaves blanketing canopies of trees. The species, their numbers, relative frequencies and relative densities are tabulated in Table 2.4. The table also contains species that were found within the study area but not included in the sampling plots.

A total of 1633 understory stems were encountered in the 15 plots that were used to characterize the understory vegetation at Kaludiyapokuna. A total number of understory species observed was 42, belonging to 37 genera and 24 families. The species, their numbers, relative frequencies and relative densities are tabulated in Table 2.5. The table also contains species that were found within the study area, but not included in the sampling plots. Of the 1633 understory stems, approximately 75 percent was constituted of species that occurred as trees in the Kaludiyapokuna forest. Of the total species that constituted the understory stand, approximately 79 percent of the species were also present as trees at Kaludiyapokuna.

2.3.5 Primate density

During the preliminary reconnaissance census, 17 sightings of *T. vetulus* and 23 sightings of *S. entellus* were made, which resulted in a density estimate of 0.8 groups/km for *T. vetulus* and 1.1 groups/km for *S. entellus*. Based on physical deformities and other external identification markers, 7 groups of *S. entellus* and 5 groups of *T. vetulus* were identified within the main study area, which was 2.2 km^2 in extent. The number of animals observed for *T. vetulus* during each sighting ranged from 1 to 8 individuals, with an average size of 3.6 (95% CI 2.5 to 4.7) per sighting, while the number of animals observed during each sighting for *S. entellus* ranged from 1 to 13, with an average of 5.3 (95% CI 3.9 to 6.6) animals per sighting (Table 2.6). The observed group sizes for *T. vetulus* in most instances were complete group counts, as individuals were not found to disperse over a wide area when feeding or resting. Hence, the group sizes presented here are representative of the actual group size of the species at the study site. On the contrary, *S. entellus* were found to scatter over a wide area during feeding and resting and hence observed group sizes reported here are likely to be incomplete group counts. Figure 2.6 depicts the frequency of observation of different group sizes for *T. vetulus* and *S. entellus*.

During the second census, 8 groups of *S. entellus* and 6 groups of *T. vetulus* were identified within the main study area. Group size ranges for *S. entellus* and *T. vetulus* were 11-22 animals and 3-15 animals respectively. Table 2.6 gives the group size and density estimates obtained for *T. vetulus* and *S. entellus* from the two census attempts. There was no significant difference in the estimates of average group size of *T. vetulus* derived from the observations made in the two census attempts (Table 2.6). On the contrary the mean group size obtained for *S. entellus* from observations made during the second census was significantly greater than the mean group size for the species estimated using data from the initial census. The number of groups of the two species estimated using the rapid survey technique was comparable with the number of groups encountered during direct counts.

Of the groups of langurs at the study site, 2 groups of *S. entellus* and 1 group of *T. vetulus* were fully habituated. The age and sex composition of these groups, and 4 other partially habituated groups of *T. vetulus,* were fully determined (Table 2.7). In the case of *S. entellus* both groups were multi-male multi-female, while in the case of *T. vetulus,* all groups were uni-male multi-female in structure.

2.4 Discussion

2.4.1 Forest diversity and composition

Historical evidence suggests that many parts of the dry zone had been cleared at different times for agriculture between 800 to 2000 years ago (Holmes, 1958). However, with the dwindling of ancient civilization in the dry zone, the region was abandoned by about 700 years ago (Dittus 1985) and hence the forest cover in the dry zone is considered to be secondary in nature (Holmes 1958).

The species diversity of tree species at Kaludiyapokuna is comparable to other dry forests in the Indian subcontinent and other parts of the world (Murphy and Lugo 1986; Parthasarathy and Karthikeyan 1997; Ramanujam and Kadamban 2001; Venkateswaran and Parthasarathy 2003; Mani and Parthasarathy 2005). According to Dittus (1977) the number of tree species in five semi-evergreen forests in Sri Lanka ranged from approximately 47 species to 69 species, while the survey of the Kaludiyapokuna forest reserve revealed 73 tree species, belonging to 58 genera and 30 families, making it one of the most diverse of the dry-zone forests surveyed in Sri Lanka to date. The tree community at Kaludiyapokuna differs in species composition and the relative abundance from the tree community at Polonnaruwa (Table 2.8). Similar differences in composition were observed in a comparison of six dry semi-evergreen forest reserves in Sri Lanka (Dittus 1977). This comparison revealed that the reserves that experienced high rainfall supported a greater diversity of tree species in comparison with forest reserves that experienced little rainfall. This suggests that local climatic conditions might influence the diversity of tree species at a given site. A similar comparison of three sub-tropical broad-leaved forests in India found that species diversity decreased with intensity of disturbance

(Rao et al., 1990). Although Kaludiyapokuna has a diverse floral assemblage in comparison with other dry forests, the tree diversity at Kaludiyapokuna is much lower in comparison with the tree diversity reported from tropical evergreen forests in Sri Lanka and other regions of the world (Murphy and Lugo 1986; Zhu 1997; Ayyappan and Parthasarathy 1999; Gunatilleke et al. 2006). The comparison of Kaludiyapokuna to Polonnaruwa and the review of literature on the evergreen dry forest of Sri Lanka reveal that there is considerable variability in the species composition and relative abundance of species and hence the dry evergreen forest cover could be considered a habitat mosaic. Habitat mosaics have been shown to be particularly important from the point of view of primate conservation, as they have been shown to harbor larger populations of primates than homogeneous primary forests (Brugiere et al. 2002).

The dominant family at Kaludiyapokuna was Euphorbiaceae. This was achieved through four species with IVI values greater than 9. Similarly, the dominant family at Polonnaruwa was Euphorbiaceae. But this dominance was largely achieved by the single species *Drypetes sepiaria*. At Kaludiyapokuna, the magnitude of the difference between the highest IVI value and the IVI value of any other species was lower in comparison with Polonnaruwa (Table 2.8) and other dry forests in India (Ramanujam and Kadamban 2001). The highest IVI value at Kaludiyapokuna was 28.3 for *Mischodon zeylanicus* followed by 25.4 for *Drypetes sepiaria* (Table 2.8). In comparison, at Polonnaruwa the highest was 55.5 for *Drypetes sepiaria* followed by 21.2 for *Vitex pinnata*. This suggests that no one species has a clear dominance over other species in the tree community at Kaludiyapokuna. In contrast, a trend towards dominance by *Drypetes sepiaria* was evident at Polonnaruwa (Dittus 1977). A comparison of three sub-tropical forests in

India showed that low equitability or high dominance was associated with disturbance (Rao et al. 1990).

Similar to other dry forests in Sri Lanka (Dittus 1977) and India (Parthasarathy and Karthikeyan 1997; Venkateswaran and Parthasarathy2003), the pattern of abundance of trees in relation to size class was characterized by a high stem count in the smaller size classes. However, the modal value of tree size at Kaludiyapokuna was smaller than the value of tree size at Polonnaruwa (Dittus 1977). Dittus (1977) attributed the scarcity of smaller sized trees to the sampling procedure that involved measuring trees greater than 5 m in height and illicit cutting of pole-sized trees by local human populations in many parts of the study area. In certain areas of the Polonnaruwa study site, trees less than 15 to 20 cm were entirely absent (Dittus 1977).

The spatial distribution of a tree species has important implications for the ecology of the plant species by impacting the reproduction of species and how plants utilize resources (Condit et al. 2000). Most trees in the Kaludiyapokuna study site showed an aggregated distribution. This means that the nearest neighborhood of a tree has a higher than average density of conspecifics (Condit et al. 2000). This contradicts the prediction of Janzen (1970), which states that a wide dispersion is a defense against predators. Species such as *Ficus microcarpa* and *Dialium ovoideum* with relatively large trunk size showed a random distribution. This pattern is similar to Polonnaruwa (Dittus 1977), where the majority of tree species were clumped in distribution and few species randomly distributed. The analysis of dispersion of trees from six different tropical forests by

Condit et al. (2000) showed that most species were aggregated. However, the degree of aggregation was weaker in larger diameter classes (Condit et al. 2000).

At Kaludiyapokuna the understory stand was largely composed of species that occurred as trees at the site. In contrast, at Polonnaruwa tree species occurring as shrubs constituted only 10.6 % of the total shrub stand (Dittus 1977).

2.4.2 Status of primates

The Recce survey method has been frequently used to estimate the abundance of primate populations in the wild, and involves using natural trails within a forest as transects (Green1978; Sterling and Rakotoarison 1998). The results of the two censuses conducted at the study site indicate that the rapid survey methods employed to determine the status of primate populations might be appropriate to determine the presence or absence and the number of groups of langurs in a forest. Transect methods have been widely used to estimate the abundance of primates in the wild (Fashing and Cords 2000; Brugiere and Fleury 2000). Although transect methods have been shown to satisfactorily estimate the number of primate groups in a given area, the method has been shown to underestimate group size (Defler and Pintor 1985; Brugiere and Fleury 2000). Brugiere and Fleury (2000) found that transect methods underestimated the average group size of *Colobus satanas* by 23 percent. This suggests that estimates on primate group size obtained from transect or similar survey methods should be regarded as preliminary.

The individual density estimate obtained from direct observation is comparable with densities reported for colobine monkeys from many study localities in Asia (see Davies 1994). However, the combined individual densities of *S. entellus* and *T. vetulus* at

Polonnaruwa (250-400 animals/Ha) were 3 to 5 times the individual density of colobines at Kaludiyapokuna. Similarly, a number of studies on wild primate populations have revealed a high degree of intersite variability in density (Oates et al. 1990; Ganzhorn 1992; Kay et al. 1997). Numerous studies have shown that food availability plays a key role in determining primate biomass and diversity (Kay et al. 1997; Stevenson 2001; Brugiere et al. 2002). In the case of colobine monkeys, it had been suggested that the availability of digestible mature leaves, a fallback resource for many colobine species determines their biomass (McKey 1978). Since then, numerous researchers have used the ratio of protein to fiber as index of leaf quality and demonstrated positive correlations between colobine biomass and this index of leaf quality at localities in Asian and African (Waterman et al. 1988; Oates et al. 1990; Chapman et al. 2002). Thus, it is possible that the difference in the biomass of colobines between Polonnaruwa and Kaludiyapokuna could be due to differences in quality of leaves available to langurs in the two localities. Differences in leaf quality could arise due to differences in the floral community between the two sites (Table 2.8). In addition, human disturbances such as hunting (Freese et al. 1982) and logging (Johns and Skorupa 1987) have been shown to negatively impact primate biomass. However, hunting and logging are unlikely causes for the differences in langur density between the two sites, as there was no indication that hunting or logging took place at Kaludiyapokuna. The patterns observed in the size class distribution of trees at Kaludiyapokuna and the low IVI values of tree species are further evidence for the absence of logging or any human induced or natural disturbances at Kaludiyapokuna. As primate biomass has been positively linked to food availability, it is possible that disposal of food refuse by local and foreign tourists within the site (Ekanayake et al. 2006) provisions the primate population at Polonnaruwa, resulting in the increase in the density of primates at the locality.

The multi-male social group was the predominant grouping pattern observed for *S. entellus* at Kaludiyapokuna. In contrast, *T. vetulus* was characterized by one-male bisexual groups. The one-male bisexual group is the predominant grouping pattern observed for *T. vetulus* in Polannaruwa and other localities in Sri Lanka (Rudran 1973a; 1973b). *S. entellus* exhibit social flexibility in relation to group size and the number of males per group in that they occur as multi-male and one-male bisexual groups (Newton 1988; Newton and Dunbar, 1994). These two grouping patterns occur in varying frequencies throughout the Indian subcontinent (Newton 1988). However, the one-male social unit is the predominant one in many study localities in India (Newton 1988; Koenig and Borries 2001). In a few study localities in northern India and in Sri Lanka, the multi-male social unit predominates (Ripley 1965; Boggess 1980; Borries1997). Studies that examine this social variation and the ecological and behavioral processes that influence langur social structure have dominated the literature on hanuman langurs. An analysis of 24 wild populations of hanuman langurs found that the number of adults was positively correlated with troop size and the number of adult females in the troop but failed to elucidate any relationship between the number of males in a group and the density of langurs, predation pressure, and economic-advantage hypotheses (Newton 1988). In addition, reproductive synchrony and home range size (distance between groups) (Srivastava and Dunbar 1996), predatory pressure (Treves and Chapman 1996) and langur population density (Moore 1999) have been shown to influence the number of males in a group.

Currently, *T. vetulus* and *S. entellus thersites* are listed as endangered in the IUCN Red List of Threatened Species (IUCN 2011). Habitat loss has been identified as the major cause for their decline (IUCN 2011). Sri Lanka lost more than 50 percent of its forest cover between 1994 and 2003 (IUCN 2011). Major development projects initiated by the government of Sri Lanka have contributed significantly to the deforestation of the island. The Mahaweli Development Scheme initiated to irrigate the dry zone replaced about 200,000 ha of natural forest with irrigation infrastructure (Steele et al. 1997). In addition, short-rotation swidden agriculture, intensive cattle grazing, and conversion into plantations and other land use types, have contributed to deforestation in Sri Lanka (Perera 2001). Although swidden agriculture has been traditionally practiced in the dry zone of Sri Lanka, high population growth in rural areas has increased the need for agricultural land (Perera 2001). Fire used in the preparation of swidden agricultural land, often escapes into adjacent forests. Frequent burning of vegetation deflects succession and promotes the growth of grasses (Perera 2001). The cultivation of tea, rubber, coffee, coconut or other permanent crops, and other types of timber harvesting has resulted in a 68% reduction in natural high forest cover between 1900 and 1983 (Perera 2001). Apart from these factors, natural phenomena such as cyclones also cause damage to forests, especially dry zone forests (Dittus 1985). All these factors have contributed to an annual deforestation rate of 3.5 percent, which places Sri Lanka as the country with the highest rate of deforestation in Asia (Dinerstein and Wikramanayake 1993). Currently, approximately 12 percent of the land cover of Sri Lanka has been designated as protected areas to conserve wildlife (Dinerstein and Wikramanayake 1993). However, it has been predicted that habitat loss will continue to occur outside the protected areas, compromising the survival of primates and other wildlife that reside outside the protected area network (Dinerstein and Wikramanayake 1993). This is particularly a concern for two subspecies of *T. vetulus*, *T. vetulus nestor* and *T. vetulus vetulus*, which occupy habitats such as home gardens which are outside the protected area system (IUCN 2011). Low-level subsistence hunting of *S. entellus* and *T. vetulus* has been reported (IUCN 2011) but is unlikely to have a major impact on the long-term survival of these species. Considering the present plight of primates in Sri Lanka and predicted rates of deforestation, urgent action is needed to secure the long-term survival of these primates in Sri Lanka.

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2.6 Tables

Table 2.1. The percent relative frequency, relative density, relative basal area and IVI of tree species. Plant families are ranked according to IVI. * = Species utilized by *S. entellus* as food, $^{\Delta}$ = Species consumed by *T. vetulus* as food, IVI= Important Value Index, BA= Basal area.

Family (no. of trees) **Species**	**% relative frequency**	**% relative density**	**% relative BA**	**IVI**
Euphorbiaceae (806)	**31**	**46.6**	**21.6**	**99.2**
*Mischodon zeylanicus**$^{\Delta}$	7.0	15.0	6.3	28.3
Drypetes sepiaria *$^{\Delta}$	6.2	7.9	11.3	25.4
Dimorphocalyx glabellus	5.2	9.0	1.9	16.1
Mallotus eriocarpus *$^{\Delta}$	4.6	8.5	0.5	13.6
*Mallotus philippensis**	4.0	4.3	0.6	8.9
Phyllanthus polyphyllus	1.4	0.8	0.1	2.3
Cleistanthus pallidus	0.9	0.6	0.2	1.7
Mallotus resinosus	0.9	0.3	0.2	1.4
*Macaranga peltata**	0.4	0.2	0.4	1.0
Sapuim sp.*	0.2	0.0	0.1	0.3
Euphorbia antiquorum	0.2	0.0	0.0	0.2
*Bridelia retusa**	-	-	-	-
*Suregada angustifolia**	-	-	-	-
Ebenaceae (343)	**13.9**	**16.2**	**10.4**	**40.5**
*Diospyros oocarpa**$^{\Delta}$	6.4	10.1	7.4	23.9
*Diospyros ovalifolia**	4.9	4.9	1.00	10.8
*Diospyros ebenum**	2.0	0.9	1.8	4.7
*Diopyros malabarica**	0.6	0.3	0.2	1.1
Sapindaceae (383)	**10.8**	**9.7**	**8.9**	**29.4**
*Lepisanthes senegalensis**$^{\Delta}$	5.9	6.5	2.0	14.4
*Dimocarpus longan**$^{\Delta}$	3.6	2.7	1.7	8.0
*Schleichera oleosa**	0.2	0.0	4.1	4.3
*Lepisanthes tetraphylla**$^{\Delta}$	1.1	0.5	1.1	2.7
Moraceae (21)	**3.00**	**0.9**	**18.9**	**22.8**
Ficus microcarpa *$^{\Delta}$	1.7	0.6	12.0	14.3
*Ficus amplissima**	0.6	0.2	6.4	7.2
Ficus mollis$^{\Delta}$	0.3	0.1	0.2	0.6
*Ficus virens**	0.2	0.0	0.2	0.4
Ficus arnottiana$^{\Delta}$	0.2	0.0	0.1	0.3
*Ficus racemosa**	-	-	-	-
*Broussonetia zeylanica**	-	-	-	-
Sterculiaceae (64)	**5.2**	**3.0**	**8.3**	**16.5**
*Pterospermum suberifolium**$^{\Delta}$	4.3	2.7	5.30	12.3
*Pterygota thwaitesii**	0.9	0.3	3.0	4.2
Annonaceae (119)	**7.1**	**5.6**	**2.4**	**15.1**
*Polyalthia coffeoides**	1.8	2.6	0.5	4.9
*Xylopia nigricans**$^{\Delta}$	3.3	2.0	1.8	7.1
Polyalthia korinti	1.8	1.0	0.1	2.9
Alphonsea sclerocarpa	0.2	0.0	0.0	0.2

(Continued)

Table 2.1. (Continued)

Lauraceae (87)	**4.0**	**4.1**	**2.2**	**10.3**
Cryptocarya sp.*	3.7	4.0	2.2	9.9
Neolitsea cassia	0.3	0.1	0.0	0.4
Tiliaceae (75)	**5.0**	**3.5**	**1.4**	**9.9**
*Grewia rothii**$^{\Delta}$	4.6	3.4	1.3	9.3
Berrya cordifolia	0.4	0.1	0.1	0.6
Grewia damine	-	-	-	-
Ulmaceae (3)	**0.5**	**0.1**	**6.7**	**7.3**
*Holoptelea integrifolia**$^{\Delta}$	0.5	0.1	6.7	7.3
Datiscaceae (11)	**1.1**	**05**	**4.6**	**6.2**
*Tetrameles nudiflora**$^{\Delta}$	1.1	0.5	4.6	6.2
Flacourtiaceae (23)	**1.7**	**1.0**	**3.30**	**6.0**
*Hydnocarpus venenata**$^{\Delta}$	1.5	1.0	3.3	5.8
Flacourtia indica	0.2	0.0	0.0	0.2
Aponogetonaceae (30)	**2.6**	**1.4**	**1.5**	**5.5**
*Wrightia angustifolia**$^{\Delta}$	2.0	1.2	1.1	4.3
*Wrightia flavido-rosea**	0.3	0.1	0.3	0.7
Wrightia tomentosa	0.3	0.1	0.1	0.5
Rubiaceae (39)	**2.8**	**1.8**	**0.6**	**5.2**
*Tricalysia dalzelli**$^{\Delta}$	2.6	1.8	0.6	5.0
Ixora sp.*$^{\Delta}$	0.2	0.0	0.0	0.2
Anacardiaceae (22)	**2.2**	**1.0**	**1.6**	**4.8**
*Nothopegia beddomei**	1.2	0.6	0.3	2.1
*Spondias dulcis**$^{\Delta}$	0.5	0.2	0.8	1.5
*Lannea coromandelica**$^{\Delta}$	0.3	0.2	0.2	0.7
*Mangifera zeylanica**	0.2	0.0	0.3	0.5
Fabaceae (18)	**2.0**	**0.8**	**1.6**	**4.4**
*Dialium ovoideum**$^{\Delta}$	1.8	0.8	1.6	4.2
*Bauhinia tomentosa**	0.2	0.0	0.0	0.2
Verbenaceae (14)	**1.9**	**0.6**	**1.3**	**3.8**
*Vitex altissima**$^{\Delta}$	1.4	0.4	1.2	3.0
*Premna procumbens**	0.5	0.2	0.1	0.8
Sapotaceae (6)	**0.7**	**0.3**	**2.0**	**3.0**
*Manilkara hexandra**$^{\Delta}$	0.6	0.2	1.6	2.4
Mimusops elengi	0.1	0.1	0.4	0.6
Clusiaceae (11)	**0.9**	**0.5**	**0.8**	**2.2**
Mesua ferrea	0.9	0.5	0.8	2.2

(Continued)

Table 2.1. (Continued)

Capparaceae (12)	**1.5**	**0.6**	**0.2**	**2.3**
Capparis zeylanica	1.5	0.6	0.2	2.3
Rutaceae (5)	**0.4**	**0.2**	**0.2**	**0.8**
Clausena dentata	0.2	0.1	0.2	0.5
Murraya paniculata	0.2	0.1	0.0	0.3
*Limonia acidissima**	-	-	-	-
Malvaceae (6)	**0.8**	**0.3**	**0.0**	**1.1**
*Abelmoschus angulosus**$^{\Delta}$	0.8	0.3	0.0	1.1
Meliaceae (3)	**0.3**	**0.1**	**0.2**	**0.6**
Aglaia elaegnoidea	0.3	0.1	0.2	0.6
Burseraceae (4)	**0.5**	**0.1**	**0.2**	**0.8**
*Commiphora caudata**$^{\Delta}$	0.5	0.1	0.2	0.8
Arecaceae (1)	**0.2**	**0.0**	**0.3**	**0.5**
*Schefflera emarginata**$^{\Delta}$	0.2	0.0	0.3	0.5
Myrtaceae (3)	**0.3**	**0.1**	**0.1**	**0.5**
Eugenia bracteata	0.3	0.1	0.1	0.5
Ochnaceae (1)	**0.2**	**0.0**	**0.0**	**0.2**
*Ochna lanceolata.**	0.2	0.0	0.0	0.2
Flagellariaceae (1)	**0.2**	**0.0**	**0.0**	**0.2**
Scolopia acuminata	0.2	0.0	0.0	0.2
Bignoniaceae				
*Stereospermum colais**	-	-	-	-
Melastomataceae				
*Memocylon sylvaticum**$^{\Delta}$	-	-	-	-
Moringaceae				
Streblus taxiodes	-	-	-	-

Table 2.2. Comparison of rank based on IVI and relative density. IVI= Important value index.

Species	**IVI**	**Rank relative density**	**Change**
Mischodon zeylanicus	1	1	0
Drypetes sepiaria	2	5	+3
Diospyros oocarpa	3	2	-1
Dimorphocalyx glabellus	4	3	-1
Lepisanthes senegalensis	5	6	+1
Ficus microcarpa	6	22	+16
Mallotus eriocarpus	7	4	-3
Pterospermum suberifolium	8	11	+3
Diospyros ovalifolia	9	7	-2
Cryptocarya sp.	10	9	-1
Grewia rothii	11	10	-1
Mallotus philippensis	12	8	-3
Dimocarpus longan	13	12	-1
Holoptelea integrifolia	14	45	+31
Ficus amplissima	15	36	+21

Table 2.3. Spatial distribution of commonly encountered tree species at Kaludiyapokuna. * = Species utilized by _S. entellus_ as food, $^{\Delta}$ = Species consumed by _T. vetulus_ as food.

Species	**n**	**(I_p)**	**(I_d) (p)**	**Conclusion**
Mallotus eriocarpus*$^{\Delta}$	179	0.519	3.311 (0.00)	Clumped
Cryptocarya sp.*	85	0.518	3.305 (0.00)	Clumped
Dialium ovoideum*$^{\Delta}$	17	-0.488	2.169 (0.05)	Random
Dimocarpus longan*$^{\Delta}$	56	0.505	2.031 (0.00)	Clumped
Dimorphocalyx glabellus	190	0.512	2.540 (0.00)	Clumped
Diospyros ebenum	20	0.508	3.105 (0.00)	Clumped
Diospyros oocarpa*$^{\Delta}$	214	0.506	1.742 (0.00)	Clumped
Diospyros ovalifolia	103	0.519	3.437 (0.00)	Clumped
Drypetes sepiaria*$^{\Delta}$	166	0.507	1.995 (0.00)	Clumped
Ficus microcarpa*$^{\Delta}$	15	-0.045	1.124 (0.41)	Random
Grewia rothii*$^{\Delta}$	72	0.514	2.885 (0.00)	Clumped
Hydnocarpus venenata*$^{\Delta}$	22	0.580	11.238 (0.00)	Clumped
Lepisanthes senegalen*$^{\Delta}$	137	0.510	2.280 (0.00)	Clumped
Mischodon zeylanicus*$^{\Delta}$	317	0.515	2.835 (0.00)	Clumped
Polyalthia coffeoides	55	0.559	2.193 (0.00)	Clumped
Polyalthia korinti	21	0.516	3.933 (0.00)	Clumped
Pterospermum suberifolium*$^{\Delta}$	57	0.512	2.736 (0.00)	Clumped
Tricalysia dalzelli *$^{\Delta}$	38	0.521	4.028 (0.00)	Clumped
Wrightia angustifolia*$^{\Delta}$	26	-0.414	1.634 (0.08)	Random
Xylopia nigricans*$^{\Delta}$	22	0.506	2.193 (0.00)	Clumped

Morisita’s index (I_d) assumes unity (1.0) for a random distribution, over 1.0 for a clumped distribution, and less than 1.0 for a uniform distribution. The Standardized Morisita Index (I_p) ranges from -1.0 to + 1.0, with 95% confidence intervals at ± 0.5. Random patterns give a value of zero, clumped patterns above zero and uniform patterns below zero. The null hypothesis of randomness was tested by computing a χ^2 statistic for index values.

Table 2.4. Number, relative frequency and relative density of liana and climber species. * = Species utilized by *S. entellus* as food, $^{\Delta}$ = Species consumed by *T. vetulus* as food.

Family Species	n	% relative frequency	% relative density
Hippocrateace			
Salacia reticulata	33	20.4	41.9
Combretaceae			
*Combretum ovalifolia**$^{\Delta}$	16	14.6	20.3
Loganiaceae			
Strychnos nux-vomica	10	14.6	12.7
Fabaceae			
*Entada pusaetha**	8	20.4	10.1
Derris scandens	3	5.8	3.8
Rhamnaceae			
*Ventilago madraspatana**	3	8.7	3.8
Annonaceae			
Artabotrys sp.	3	5.8	3.8
Annonaceae			
Uvaria macropoda	1	2.9	1.3
Linaceae			
*Hugonia ferruginea**	1	2.9	1.3
Olacaceae			
Olax sp.	1	2.9	1.3
Opiliaceae			
*Opilia amentacea**$^{\Delta}$	-	-	-
Menispermaceae			
*Tiliacora acuminata**	-	-	-
Apocynaceae			
*Carissa inermis**	-	-	-
Asteraceae			
*Mikenia scandens**	-	-	-

Table 2.5. Number, relative frequency and relative density of understory species. • = Species which occurred as trees at Kaludiyapokuna.

Family **Species**	**n**	**% relative frequency**	**% relative density**
Euphorbiaceae			
Mischodon zeylanicus •	355	6.5	21.7
Dimorphocalyx glabellus•	81	4.3	5.0
Mallotus philippensis•	55	5.6	3.4
Drypetes sepiaria•	53	6.0	3.2
Mallotus eriocarpus•	31	2.2	1.9
Cleistanthus pallidus•	20	3.3	1.2
Phyllanthus polyphyllus•	8	0.4	0.5
Euphorbia antiquorum•	1	0.4	0.1
Flueggea leucopyrus	1	0.4	0.1
Rutaceae			
Glycosmis pentaphylla	353	6.5	21.6
Atalantia ceylanica	3	1.3	0.2
Murraya paniculata•	3	0.4	0.2
Ebanaceae			
Diospyros oocarpa•	172	5.6	10.5
Diospyros ovalifolia•	83	6.1	5.1
Diospyros malabarica•	1	5.6	0.1
Sapindaceae			
Lepisanthes senegalensis•	131	6.1	8.0
Democarpus longan•	20	3.5	1.2
Lepisanthes tetraphylla•	7	2.2	0.4
Madhuca longifolia	1	0.4	0.1
Annonaceae			
Polyalthia coffeoides•	118	6.1	7.2
Polyalthia korinti•	1	0.4	0.1
Sterculiaceae			
Melochia corchorifolia	20	0.4	1.2
Pterospermum suberifolium•	14	3.0	0.8
Rubiaceae			
Psilanthus whghtianus	17	3.0	1.0
Tricalysia dalzelli•	12	2.6	0.7
Mitragyna parvifolia	1	0.4	0.1
Canthium coromandelicum	-	-	-
Capparidaceae			
Capparis zeylanica•	18	3.5	1.1
Crateva adanasonii	1	0.4	0.1
Moraceae			
Streblus toxoides•	13	2.2	0.8
Ficus microcapa•	1	0.4	0.1

(Continued)

Table 2.5. (Continued)

Melastomataceae			
Memecylon sylvaticum•	9	1.7	0.6
Myrtaceae			
Eugenia bracteata•	6	1.7	0.4
Boraginaceae			
Carmona retusa	4	0.9	0.2
Clusiaceae			
Mesua ferrea•	\4	0.4	0.2
Rhamnaceae			
Scutia myrtina	4	1.7	0.2
Anacardiaceae			
Nothopegia beddomei•	3	1.3	0.2
Meliaceae			
Aglaia elaegnoidea•	3	0.9	0.2
Fabaceae			
Bauhinia recemosa•	1	0.4	0.1
Malvaceae			
Hibiscus eriocarpus	1	0.4	0.1
Ochnaceae			
Ochna lanceolata•	1	0.4	0.1
Tiliaceae			
Grewia rothii•	1	0.4	0.1
Verbenaceae			
Vitex altissima •	1	0.4	0.1
Lamiaceae			
Basilicum polystachyon	-	-	-

Table 2.6. Average group size and density of *S. entellus* and *T. vetulus* at Kaludiyapokuna based on the initial reconnaissance survey.

Census	n		Mean group size ($\bar{x}$) (CI)		Density (animals/ km^2)	
	T. vetulus	*S.entellus*	*T. vetulus*	*S. entellus*	*T. vetulus*	*S. entellus*
1	5	7	3.6 (2.5 4.7)	5.3 (3.9 6.6)	8.10	16.70
2	6	8	7.0 (1.8 12.1)	14.7 (11.8 17.7)	19.10	53.40

Table 2.7. Composition of study groups and other groups encountered within the study area. AM= Adult male, AF= Adult female, SA= Subadult, JV= Juvenile, IN = Infant, * = habituated groups.

Species		AM	AF	SA	JV	IN	Total
S. entellus	S1	3	7	3	7	2	22*
	S2	2	5	1	5	1	13*
	S3	-	-	-	-	-	13
	S4	-	-	-	-	-	11
	S5	-	-	-	-	-	17
	S6	-	-	-	-	-	15
	S7	-	-	-	-	-	15
	S8	-	-	-	-	-	12
T. vetulus	T1	1	6	0	0	4	11*
	T2	1	8	-	-	-	15
	T3	1	2	0	1	1	5
	T4	1	2	0	1	1	5
	T5	1	1	0	0	1	3
	T6	1	2	0	0	0	3

Table 2.8. A comparison of woody tree diversity and composition between Kaludiyapokuna and Polonnaruwa. * = Derived from Dittus (1977).

	Kaludiyapokuna	Polonnaruwa*
Area sampled	2.36 Ha	18.25 Ha
Number of species	75	61
Genera	58	50
Families	30	25
Most important species (IVI)		
	Mischodon zeylanicus (36.30)	*Drypetes sepiaria* (55.50)
	Drypetes sepiaria (27.02)	*Vitex pinnata* (21.20)
	Diospyros oocarpa (21.28)	*Schleichera oleosa* (21.10)
	Dimorphocalyx glabellus (19.95)	*Premna tomentosa* (20.00)
	Allophylus serratus (17.47)	*Grewia polygama* (19.60)
	Diospyros ovalifolia (17.12)	*Cassia fistula* (13.20)
	Lepisanthes senegalensis (14.96)	*Adina cordifolia* (12.80)
	Ficus microcarpa (13.18)	*Cassia roxburghii* (11.00)
	Pterospermum suberifolium (10.71)	*Lepisanthes tetraphylla* (10.30)
	Cryptocarya sp. (10.28)	*Strychnos potatorum* (10.00)
	Mallotus philippensis (9.18)	*Ixora arborea* (9.60)
	Grewia rothii (8.12)	*Manilkara hexandra* (9.50)
	Dimocarpus longan (6.99)	*Ficus amplissima* (8.70)
	Holoptelea integrifolia (6.97)	*Walsura piscidia* (8.50)
	Ficus amplissima (6.77)	*Syzigium cumini* (6.8)

2.7 Figures

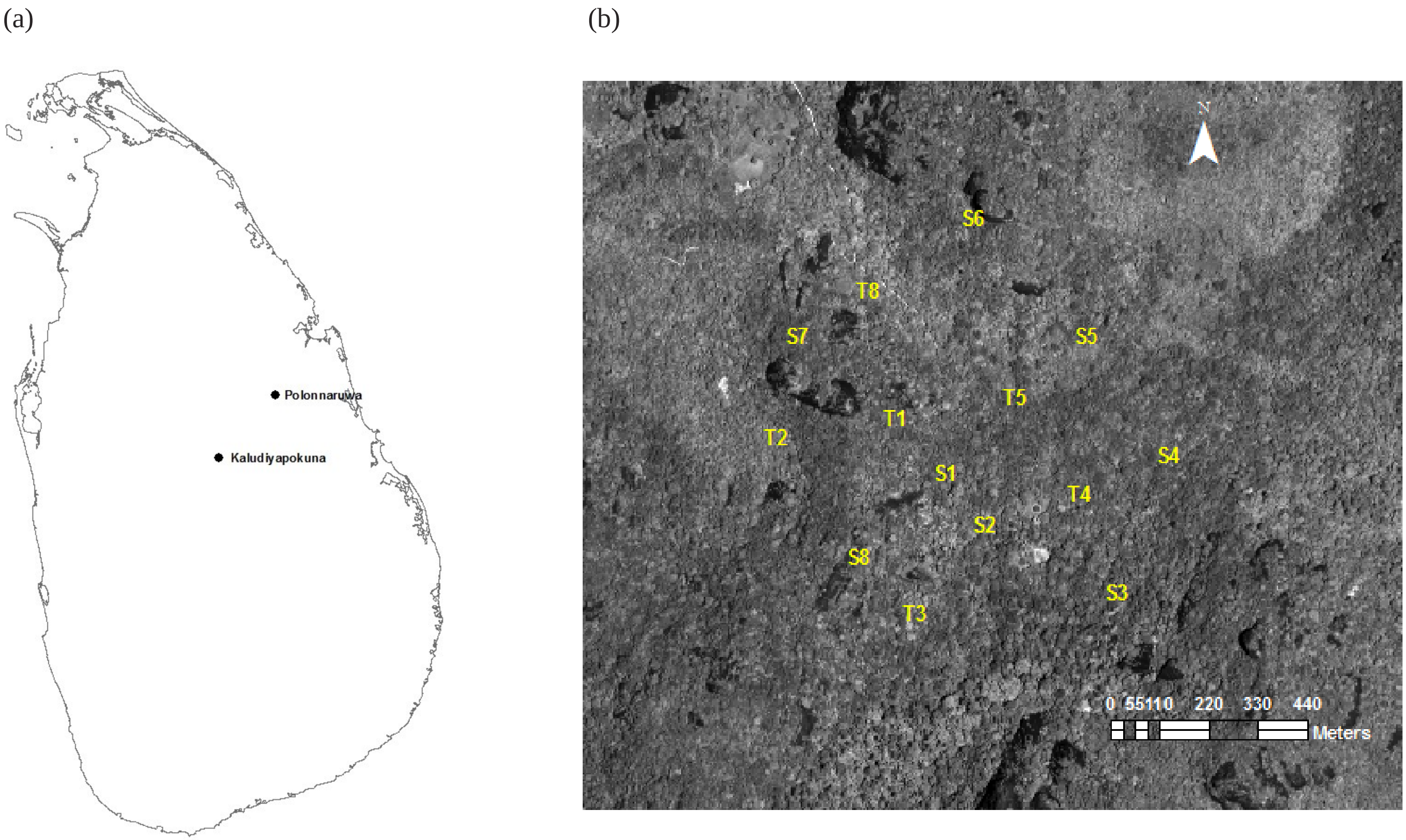

Figure 2.1. (a) Map of Sri Lanka depicting the location of the study site, (b) locations of the troops of primates encountered during the study period.

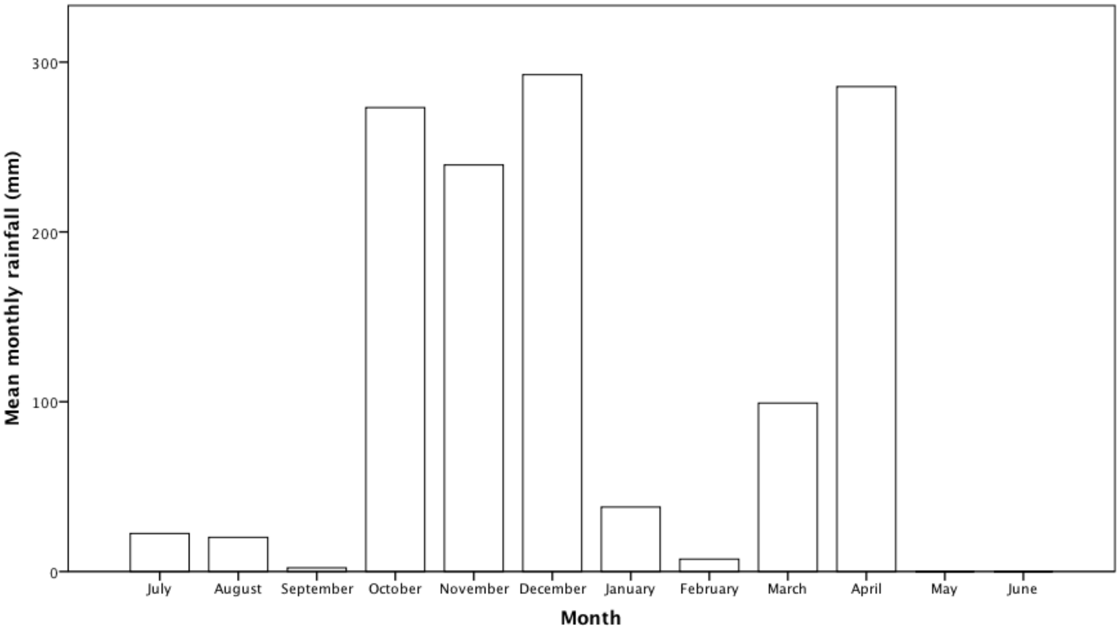

Figure 2.2. Rainfall pattern at Kaludiyapokuna during July 2008 to June 2009 showing peaks in October and December and March and April. Notably the driest months produced almost no rainfall.

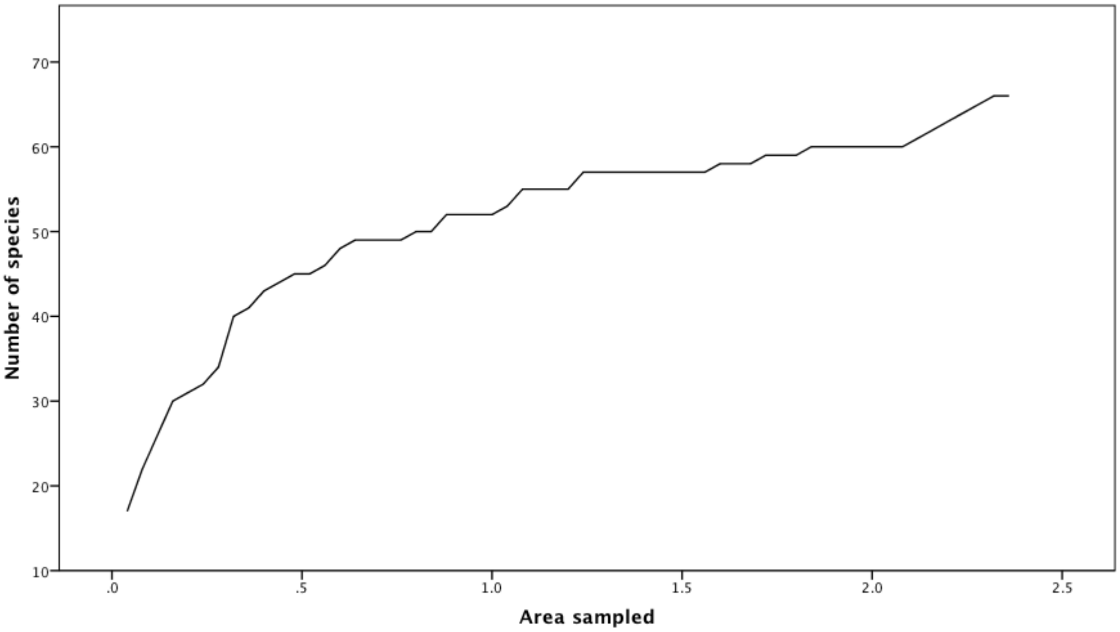

Figure 2.3. Species area curve for tree species at the Kaludiyapokuna forest reserve.

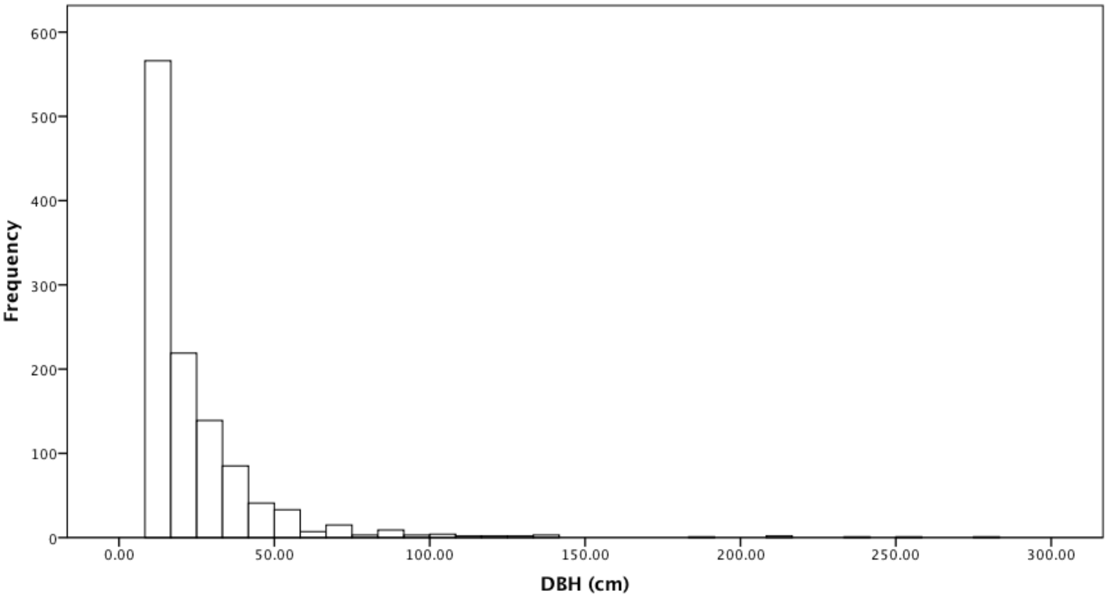

Figure 2.4. Number of individuals per size class of diameter at breast height.

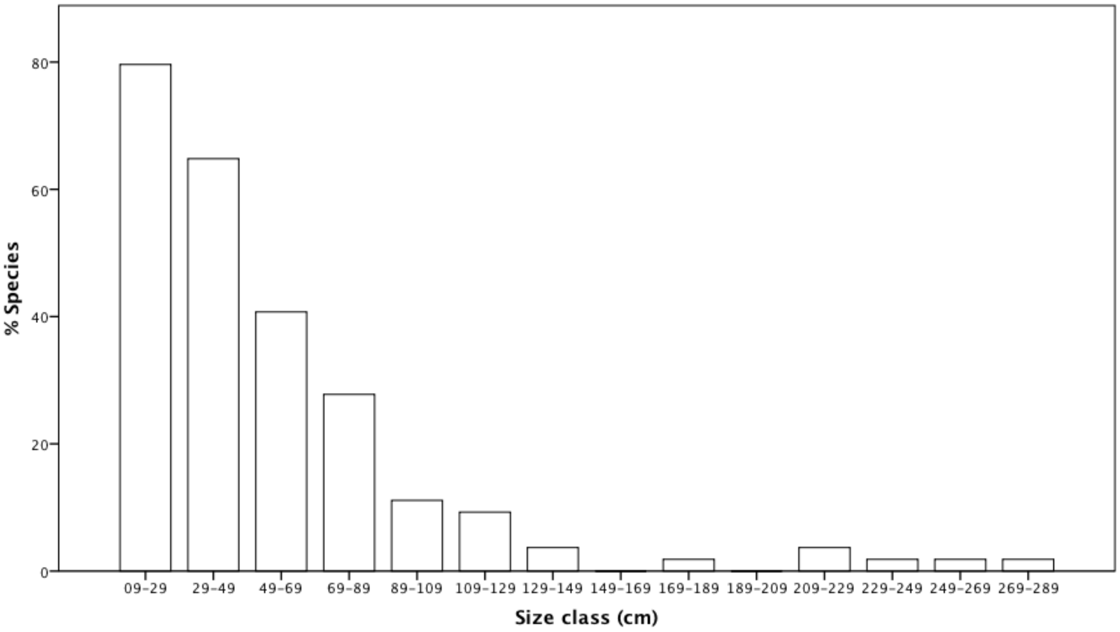

Figure 2.5. The percentage of tree species per size class.

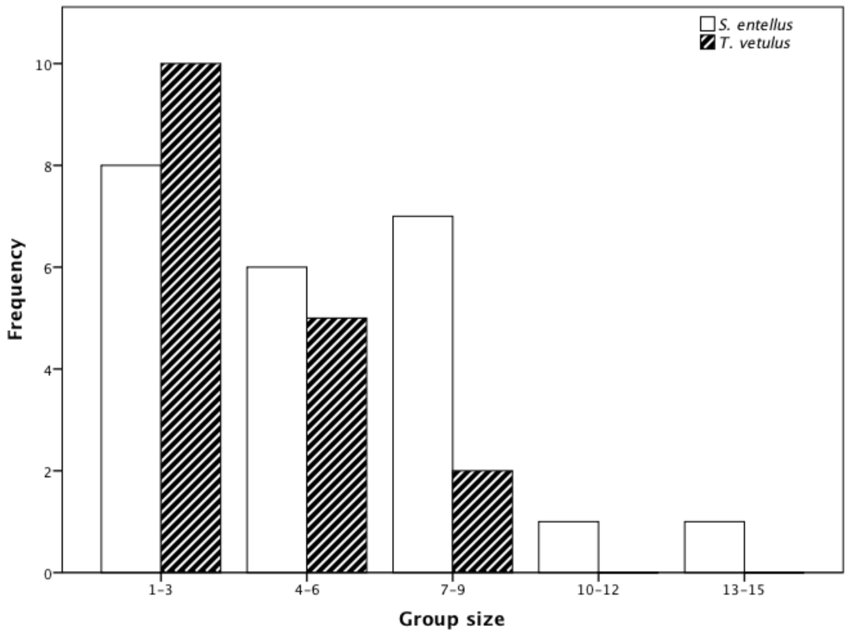

Figure 2.6. Frequency of observation of group sizes of *S. entellus* and *T. vetulus*.

Chapter 3

Dietary diversity and food selection in *Trachypithecus vetulus* and *Semnopithecus entellus* in the Kaludiyapokuna forest reserve in the dry zone of Sri Lanka.

3.1 Introduction

Understanding how the diets of primates vary in relation to spatiotemporal variation in food availability is a fundamental question in primatology (Hladik 1977; Fashing 2001; Chapman and Chapman 1999). Due to the ability of colobine monkeys to ingest large quantities of foliage, their dietary ecology has been of particular interest to primatologists (Struhsaker 1975; Oates 1988; Newton 1992). Although colobine monkeys have been traditionally described as strict folivores (Ripley 1970; Wrangham 1980), an increasing number of studies have shown that considerable interspecific variation exists. While leaves have been shown to comprise a significant proportion of the diet of some species (Oates 1988; Hladik 1977), fruit (Fashing 2001; Dela 2007) and seeds (McKey et al. 1981; Maisels et al. 1994) have been shown to be important components of the diets of other colobines. In addition to interspecific differences, there is considerable evidence that also points to intraspecific diet variation in colobine monkeys (Chapman and Chapman 1999; Chapman et al. 2002). Despite this evidence, data stemming from a few studies from a single study area are often used to characterize the feeding ecology and the mechanisms of coexistence in sympatric colobines, as in the case of *Semnopithecus entellus* (Hanuman langur) and *Trachypithecus vetulus* (purple-faced langur) (Hladik 1977).

The availability and the spatial distribution of food resources have been shown to influence the intensity of within-group competition in primates, and hence have been identified as important elements influencing the socioecology of primates (Wrangham 1980; van Schaik 1989; Chapman et al. 1995). It has been predicted that, when animals feed on clumped food resources of intermediate size relative to group spread, within-group contest competition should occur (Koenig et al. 1998; van Schaik 1989). In the event animals feed on resources that are dispersed in space and are of similar quality, or when patches are large enough to accommodate all the members of a group, competition is thought to be within-group scramble or absent (Wrangham 1980; Koenig et al. 1998; van Schaik 1989; Isbell 1991). Although a number of studies have presented evidence for the presence of within-group competition in colobines (Koenig 2000; Gillespie and Chapman 2001), relatively few studies have attempted to quantify the spatial distribution and the abundance of food resources used by colobine monkeys to determine the potential for competition (Koenig et al. 1998; Grueter et al. 2009)

Much of what is known about the ecology of forest dwelling *S. entellus* and *T. vetulus* in Sri Lanka is from Polonnaruwa, a heavily disturbed secondary dry zone forest, where these primates occur sympatrically. These studies have focused on the social organization and reproduction of *T. vetulus* (Rudran 1973a; 1973b), social organization and general ecology of *S. entellus* (Ripley 1965; 1967; 1970) and feeding behavior of sympatric *T. vetulus* and *S. entellus* in relation to phenology (Hladik 1977). In these studies, it was noted that at Polonnaruwa, *S. entellus* was less arboreal and utilized a more diverse array of plants than *T. vetulus*. Both species were found to ingest different proportions of fruits, flowers and leaves, and varied the intake of these items according to their availability in the environment. However, *T. vetulus* was found to be more folivorous than *S. entellus* throughout the study period and of the leaves consumed by *T. vetulus*, two-thirds (40% of all food ingested) were mature leaves. The dietary items consumed by *S. entellus* were also found to be high in protein in comparison to the diet of *T. vetulus*. This prompted Hladik (1977) to conclude that low mobility associated with *T. vetulus* at Polonnaruwa is an adaptation to minimize energy expenditure to survive on a diet of low nutritional value. More recently, a study on *T. vetulus* living in human-modified habitats in the Western Province of Sri Lanka showed that over 80% of diet of the species consisted of seasonal plant parts (fruit, flowers and immature leaves) (Dela 2007).

This chapter provides quantitative data on feeding ecology of two free-ranging groups of *S. entellus* and a free-ranging group of *T. vetulus* in a relatively undisturbed dry zone forest in the north central dry zone of Sri Lanka. Specifically, this study compares and contrasts the monthly percentage of time devoted to feeding by *S. entellus* and *T. vetulus* on specific dietary items in relation to their availability. This study also examines dietary niche breadth of the two species in an attempt to determine if the ecological differences observed in these species at Polonnaruwa can be generalized to explain the coexistence of the study groups of these species at the Kaludiyapokuna forest reserve. Additionally, the study also quantifies the spatial distributions and the relative abundance of key resources utilized by these primates, to determine the potential for intraspecific and interspecific interactions in these primates.

3.2 Material and methods

3.2.1 Study site

The study was conducted in the Kaludiyapokuna forest reserve (N 07° 52.5, E 080° 44.1) located in the Matale district in the north central dry zone of Sri Lanka. The study was conducted under the authority of the Department of Wildlife Conservation of Sri Lanka and in collaboration with the University of Peradeniya, Sri Lanka. The main study area is approximately 2.2 km^2 in extent and is contiguous with the Knuckles forest range in the south. The study site is surrounded by farmland and human settlements from the north, east and west. The study site is undisturbed by humans and the primates are not provisioned, unlike the Polonnaruwa study site, which is disturbed and where primates have become accustomed to humans through regular contact (Bishop et al. 1981). Also there is no evidence to indicate that hunting, timber extraction or woodcutting has occurred at the site. The study site supports populations of four species of primates as well as populations of other herbivorous mammals such as Asian elephants (*Elephas maximus*), spotted deer (*Axis axis*), sambar deer (*Cervus unicolor*), and wild pig (*Sus scrofa*). Unlike Polonnaruwa (Bishop et al. 1981), this study area is home to a full complement of potential primate predators such as the black eagle (*Ictinaetus malayensis*), leopard (*Panthera pardus*) and python (*Python molurus*).

The study area receives about 1250 mm of rainfall annually (Fig. 3.1) and average temperature in the region ranges between 27-29 º C. The region receives most of its rainfall through convectional rains from October to November, which gradually grade into the northeast (NE) monsoon. The NE monsoon lasts from December to February and is most active during the month of December. The NE monsoon brings considerably less moisture than the southwestern (SW) monsoon, which lasts May to September. The northern dry zone is shielded from the SW monsoon rains by the central hills of the island and hence it experiences a characteristic period of drought during this time.

3.2.2. Subjects

In Sri Lanka, *S. entellus* is represented by a physically smaller subspecies *S. entellus thersites* (Bennett and Davies 1994) and is found throughout the well-wooded areas of the entire dry zone from south of Jaffna, in the North, to the shores of the extreme southern coast (Phillips, 1935). The purple-faced leaf monkey, *T. vetulus* is endemic to Sri Lanka and is divided into four distinct subspecies all occupying different geographic regions. *T. vetulus philbricki,* the northern dry zone subspecies, shares its range with *S. entellus.*

Dietary data were collected over a 12-month period between July 2008 and June 2009 as part of a long-term study initiated on the comparative ecology of *T. vetulus* and *S. entellus* in Sri Lanka. Data collection was confined to two groups of *S. entellus* and one group of *T. vetulus*. At the time of data collection, all groups were habituated to human observers and could be approached to within a distance of 10 m without showing signs of alarm. The composition of the study groups at the end of the study period is given in Table 3.1.

Groups A and B were neighboring groups with overlapping home ranges. Similarly, Group A and *T. vetulus* were neighboring groups with substantially overlapping home ranges (Fig. 3.2). The home range of *T. vetulus* also overlapped with the home ranges of three other *S. entellus* groups that were not part of this study. Group B and *T. vetulus* did not have overlapping home ranges.

3.2.3 Forest composition

Vegetation sampling was carried out using vegetation plots (Ganzhorn 2003). Localities for sampling were chosen with the aid of a WorldView 1 satellite image of the study area and care was taken to ensure that the localities were evenly distributed across the study area so that an unbiased representative sample of the vegetation could be obtained. Each plot was 20 x 20 m in extent and 59 plots were used to sample the vegetation at the study site. The trees that were greater than 9 cm in diameter at breast height (DBH) and woody lianas were measured using a DBH tape. Plant samples were collected and herbarium sheets were prepared and the specimens were identified and compared to voucher specimens at the National Herbarium at the Royal Botanical Gardens, Peradeniya, Sri Lanka. The basal area (BA) for each tree was calculated using the formula:

$BA = [0.5 \times DBH]^2 \times \pi$.

The measure BA per hectare was used to define the biomass of each plant species within the home range of each group (Fashing 2001).

The spatial distribution of resources was characterized using the Morisita (I_d) and Morisita (I_p) (Krebs 1999). Morisita’s index (I_d) assumes unity (1.0) for a random distribution, and is greater than 1.0 for a clumped distribution, and less than 1.0 for a uniform distribution. The Morisita (I_p) ranges from -1.0 to + 1.0, with 95% confidence intervals at +0.5 and -0.5. Random patterns give a value of zero, clumped patterns give a value greater than zero and uniform patterns a value below zero. The null hypothesis of randomness was tested by computing a χ^2 statistic for index values (Krebs 1999).

3.2.4 Forest phenology

To produce a quantitative measure of food availability, 958 trees and lianas in 22 phenological plots were monitored each month for phenological activity. The plant species monitored included species that were known to be consumed by the primates as well as species that were not known food species. Phenological assessment of trees was carried out with the help of two field assistants during the first week of each month. The crown of each tree was scanned using Nikon 8 x 40 binoculars by the investigator and the two field assistants for the availability of fruits, flowers and immature leaves. On occasions, it was difficult to distinguish between ripe and unripe fruit due to poor visibility and in the case of species like *Mischodon zeylanicus*, *Diospyros oocarpa*, *Hydnocarpus venenata*, and *Lepisanthes senegalensis*, due to fruit that did not show any changes in coloration or texture over time. Hence, ripe fruit and unripe fruit were pooled as fruit for the purpose of estimating fruit availability. Similarly, flower buds and flowers were pooled as flowers and leaf buds and young leaves were pooled as immature leaves. Each plant part was scored at increments of 0.5 on a scale of 0.0 to 4.0 with 4 being the score for a tree with the plant part at its greatest abundance in comparison to and with individuals of the same species in the phonological plots. For the study area, a food availability index (FAI) for fruit, flowers and immature leaves was computed using the average monthly phenological scores and the basal area/ha value for trees within the vegetation plots in the study area (Dasilva 1994). FAI was computed using the formula:

FAI = average availability score x basal area of species *i*

The species used in the computation of FAI fruit, flowers and immature leaves within the study area accounted for the 15 most frequently utilized tree species by these primates and accounted for approximately 80% of the feeding time of Groups A and B and 74% of the feeding time of *T. vetulus*.

3.2.5 Behavioral data collection

For 5-8 days a month for each of the groups, behavioral data were collected using a scan sampling technique (Altmann 1974). Each scan lasted approximately 3 minutes and scans were conducted every 10 minutes. Efforts were made to include as many adult monkeys as possible in each scan. During each scan the number of animals engaged in feeding, moving, resting and in social behaviors were recorded. When an animal was spotted, the first activity that lasted longer than 3 seconds was recorded. h minimized the overrepresentation of eye catching ephemeral activities in the data (Fashing 2001). Feeding was considered to be any instance that involved a monkey attempting to ingest, masticate or swallow a food item. When a monkey was observed to feed during a scan, the plant species and the food item on which the animal was feeding was recorded. Food items were designated as fruit, seeds, flowers, immature leaves, and mature leaves. Sap and soil were both recorded as other. During sampling, features such as pelage color, tail length in relation to body length, and anatomical deformities such as scars were used to identify individuals and minimize resampling individuals during the process.

Dietary niche breadth was estimated using Levins’s Measure, *B* (Krebs 1994) using the formula:

$$B = \frac{1}{\sum P_j^2}$$

where P_j is the proportion of items in the diet that are of the food category J.

Forage ratios (w_i) (Krebs 1999) were calculated for each dietary item (fruit, flowers and immature leaves) of a plant species utilized by the primates to measure dietary selectivity for each item. Forage ratios (w_i) were computed using the formula:

$$w_i = \frac{o_i}{p_i}$$

where o_i is the proportion of species i in the diet and p_i is the percentage of species i available in the environment. Stem density derived from the vegetation plots was used as a measure of availability of the species in the environment. The forage ratios range from 0 to ∞ and values greater than 1.0 indicate preference while values less than 1.0 indicate avoidance.

Temporal patterns of food resource use in relation to food availability were investigated by calculating Spearman rank-order correlation coefficients (r_s) between food item consumption and food item availability measured as FAI. Similarly, temporal patterns of niche separation were investigated by calculating Spearman rank-order correlation coefficients (r_s) between fruit, flower and immature leaf availability overlap and fruit, flower and immature leaf availability.

3.3 Results

3.3.1 Forest composition

In the 59 plots that were used to characterize the vegetation at the Kaludiyapokuna forest reserve, a total of 2110 trees were encountered from 73 species, belonging to 58 genera and 30 families. The DBH of trees at Kaludiyapokuna ranged from 9.0 cm to 275.2 cm with a mean and mode of 24.4 cm (SD ± 23.61) and 9.0 cm respectively. Table 3.2 gives the tree species composition within the home ranges of the three primate groups.

3.3.2 Forest phenology

The availability of fruit, flowers and immature leaves measured as FAI units/ha, varied considerably from month to month (Fig. 3.3). Fruit availability was lowest during the month of March and highest during the month of June. The availability of flowers was highest during the month of August and lowest during December and January. Immature leaf availability was at its lowest during the month of February and highest during September. Mature leaves were the most abundant food item available throughout the year.

3.3.3 Diets of S. entellus and T. vetulus

Approximately 63% the diet of *T. vetulus* consisted of leaves, whereas leaves accounted for approximately 53% of the diet of Group A and 57% of the diet of Group B of the two *S. entellus* groups respectively (Table 3.3). Immature leaves accounted for a greater proportion of the leaf intake of both species, with *T. vetulus* spending approximately 10% and 20% more time feeding on immature leaves than Groups A and B did respectively. Group A spent a small proportion (0.41%) of feeding time on sap and soil. Although not represented in the scan samples, activities such as drinking at shallow ponds in the ground did occur infrequently in the case of *S. entellus*. Drinking and geophagy were never observed in *T. vetulus*. None of the groups were observed to make deliberate efforts to feed on insects or other forms of animal matter though it is possible that the monkeys ingested insects when feeding on flowers and fruit such as figs. In the case of Group A and Group B, seasonal resources such as fruit and flowers accounted for 47% and 43% of their diets respectively. In comparison, only 31% of the diet of *T. vetulus* during the study period consisted of fruits and flowers.

Table 3.4 gives the monthly variation in the percentage of time based on scan sample records devoted to feeding on different food items. In the case of Group A, the monthly time spent feeding on fruit ranged from 2.0% to 59.0%, while in Group B the monthly time spent on feeding on fruit ranged from 0.0% to 69.0%. In comparison, the monthly time spent feeding on fruit in *T. vetulus* ranged from 0.0% to 79.0%. There was no statistically significant difference in the monthly percentage of time spent feeding on fruit (Friedman's two-way analysis of variance by ranks χ^2 (2) = 0.50, $p \leq 0.779$) between the three groups. In the case of Group A, the monthly time spent feeding on flowers ranged from 0.0% to 60.0%. The monthly time spent feeding on flowers ranged from 0.0% to 26.5% in Group B. In comparison, the monthly time spent feeding on flowers ranged from 0.0% to 40.7% in *T. vetulus*. The differences in the monthly percentage of time spent feeding on flowers by the three groups were statistically significant (Friedman's two-way analysis of variance by ranks χ^2 (2) =6.62, $p \leq 0.037$). However, monthly differences in the time spent feeding on immature leaves (Friedman's two-way analysis of variance by ranks χ^2 (2) =2.17, $p \leq 0.338$) and mature leaves (Friedman's two-way analysis of variance by ranks, χ^2 (2) = 5.71, $p \leq 0.058$) by the three groups were not statistically significant.

The contribution of different plant species and plant parts towards the diets of Groups A and B and *T. vetulus* are presented in Tables 3.5.A-C. Group A fed on 58 positively identified species, while group B fed on 32 positively identified species. In comparison, *T. vetulus* fed on 31 positively identified species. The top 10 most frequently utilized plant species by Groups A and B accounted for 70% and 72% of their diets respectively. In comparison, the top 10 most frequently utilized plant species by *T. vetulus* accounted for 76% of the diet of the group. Group A and B fed on the fruit of 20 and 13 plant species respectively, while *T. vetulus* fed on the fruit of 17 species. Similarly, Groups A and B fed on the flowers of 20 and 18 plant species respectively, while *T. vetulus* fed on the flowers of 8 species.

The proportion of time spent feeding on fruits and flowers each month by Groups A and B and *T. vetulus* was positively correlated to their monthly FAI scores (Table 3.6; Fig. 3.4). There was no statistically significant relationship between monthly consumption of immature leaves and monthly availability of immature leaves for all three groups.

There was also a significant negative correlation between monthly total leaf consumption and monthly fruit availability for Group B and *T. vetulus* (Table 3.8). Although there was a negative correlation between total leaf consumption and the availability of flowers for all three groups, no relationship was statistically significant (Table 3.9). In the case of Group A, monthly mature leaf consumption showed a statistically significant negative correlation with immature leaf availability. Although monthly mature leaf consumption was negatively correlated with immature leaf availability for Group B and *T. vetulus,* the relationships were not statistically significant.

3.3.4 Dietary diversity and food selection

The mean monthly niche breadth (*B*) was 6.42 (range 3.0-11.1) for Group A was and 5.49 (range 1.5-9.9) for Group B and 5.08 (range 2.5-7.7) for *T. vetulus*. The monthly difference in niche breadth between the three groups was not statistically significant (Friedman's two-way analysis of variance by ranks χ^2 (2) = 2.68, $p \leq 0.262$).

The forage ratios for food items from different plant species accounting for ≥ 1% of the annual diets of the study groups are listed in Tables 3.8 and 3.9. In the case of Group A, plant parts of 13 of the 20 plant species that accounted for ≥ 1% of the annual diet were preferred by the group. Similarly, Group B preferred the plant parts of 12 of the 20 species that accounted for ≥ 1% of the annual diet of the group. In comparison, *T. vetulus* selected the plant parts of 12 species of the 21 species that accounted for ≥ 1% of the annual diet of the group. The preferred species accounted for 58%, 70% and 63% of the annual diet of Group A, Group B and *T. vetulus* respectively. Based on selection ratios, plant parts of *Mischodon zeylanicus,* which accounted for a significant proportion of the annual diets of Group A and *T. vetulus* were not preferred by these two groups. Group B, which fed on the fruit, flowers and immature leaves of *Mischodon zeylanicus*, preferred only the immature leaves of the species. Similarly, the plant parts of the food species *Drypetes sepiaria,* which constituted a significant proportion of the annual diets of *S. entellus* and *T. vetulus* were not preferred by both species of primates. According to the forage ratio, Group A preferred only a single tree species (*Grewia rothii*) and B preferred two tree species (*Grewia rothii* and *Mischodon zeylanicus*) that were listed in the top 10 most abundant plant species in terms of relative density in the study areas. In comparison, none of the species preferred by *T. vetulus* were listed in the top 10 most abundant plant species in the study area.

3.4 Discussion

Groups A and B at Kaludiyapokuna consumed items from 58 and 32 species of plants respectively, while *T. vetulus* consumed 31 identified plant species. Although the number of species of food plants is likely to be correlated with observation time, the number of species consumed by *T. vetulus* and *S. entellus* is comparable with the number of species utilized by a number of colobine species as food (Table 3.10). The proportion of fruit and flowers in the diet of *T. vetulus* at Kaludiyapokuna is similar to the diet of the species at Polonnaruwa. However, at Polonnaruwa two thirds of the leaves consumed (40% of overall diet) by *T. vetulus* were mature leaves (Hladik 1977) while at Kaludiyapokuna *T. vetulus* fed predominantly on immature leaves. In comparison to the diet of *T. vetulus nestor* (Dela 2007) in the Western Province of Sri Lanka, the study group at Kaludiyapokuna consumed a significantly lower proportion of fruit but consumed a higher proportion of flowers. In terms of fruit consumption, the diet of *S. entellus* at Kaludiyapokuna is similar to the diets of *S. entellus* reported from other localities in the Indian subcontinent, but showed a tendency to include a higher proportion of flowers in its diet in comparison with *S. entellus* at other localities. In addition, *S. entellus* at Kaludiyapokuna were never observed to feed on insects as reported for *S. entellus* in India (Newton 1992; Koenig and Borries 2001).

Previous studies contrasting the feeding ecology of sympatric *T. vetulus* and *S. entellus* have reported *S. entellus* to feed on seasonal foods from a diverse array of plant species and *T. vetulus* to feed on a few plant species and include a higher percentage of mature leaves in its diet year-round (Hladik 1977). When comparing the interspecific differences in dietary diversity of the groups in this study, the difference in food plant use of Group A and *T. vetulus* in this study are similar to the differences observed between the two species at Polonnaruwa (Hladik, 1977). Like *S. entellus* at Polonnaruwa, Group A fed on a diverse array of plant species while *T. vetulus* fed on a few species (Table 3.10). However, this difference is not evident when comparing food plant use by Group B and *T. vetulus* in this study, which suggests that the two species have a high degree of ecological flexibility. In addition, contrary to the findings of Hladik (1977), *S. entellus* and *T. vetulus* in this study did not differ in their monthly intake of seasonal items such as fruit, seeds and immature leaves. *T. vetulus* and *S. entellus* at Kaludiyapokuna only differed marginally in their consumption of flowers, with *S. entellus* being more florivorous than *T. vetulus*.

Unlike in Polonnaruwa, *T. vetulus* and *S. entellus* did not differ in their consumption of mature leaves. Although less frugivorous than *T. vetulus nestor, T. vetulus* in this study exhibits similar dietary patterns to *T. vetulus nestor* in that the diet of the group consisted predominantly (95%) of seasonal plant items such as fruit, seeds, flowers and immature leaves (Dela 2007). Thus, the notion that coexistence between *S. entellus* and *T. vetulus* is facilitated by *T. vetulus* adapting to a diet of low nutritional value (mature and immature leaves) is not directly applicable to explain the coexistence of the two species at the Kaludiyapokuna forest reserve. Additionally, when comparing the dietary ecology of these two species with other published works on the two species (Table 3.10), it is apparent that intraspecific variation in dietary ecology is much greater than interspecific variation. This suggests that the differences in feeding ecology reported for the two species are most likely driven by local habitat conditions.

Asian colobines in general have been suggested to subsist primarily on leaves (Kirkpatrick 2007), and it is a central tenet in socio-ecological models describing group size and social interactions in colobines (Wrangham 1980; Janson and Goldsmith 1995; Steenbeek and van Schaik 2001). Although the annual dietary profiles of both species appear to fit this description, the statement tends to be misleading when considering the monthly variation in fruit and flower consumption of both species. During several months fruits and flowers collectively accounted for over 40% of the diet of both species and in some months exceeded leaf consumption (Table 3.5). In addition, feeding time has been shown to underestimate the mass of fruit ingested (Hladik 1977).

In the case of *T. vetulus* and *S. entellus* in this study, both species consumed fruits and flowers in proportion to their availability and did not eat immature leaves according to their availability suggests that fruit and flowers may have been the preferred foods for both species. This statement is further strengthened because Group B and *T. vetulus* fed on leaves mostly when fruit availability was low. Although previous studies on the dietary ecology of *S. entellus* have shown the species to ingest significant quantities of seasonal plant parts such as fruits, flowers and immature leaves according to availability (Newton 1992; Sayers and Norconk 2008), *S. entellus* in this study showed a tendency to prefer fruit and flowers even when immature leaves were available. The assertion that the monkeys in this study prefer fruit and flowers is largely suggestive, as food preference can be reliably tested only when all food items are equally and simultaneously available to the monkeys, conditions that are virtually impossible to meet in primate field studies. Although the colobine monkeys in this study showed a preference for fruit and flowers over leaves, species such as *Trachypithecus leucocephalus* (Li and Rogers 2006) and *Rhinopithecus bieti* (Xiang et al. 2007) showed a tendency to consume immature leaves even when fruits and flowers were available.

The forage ratios computed for plant parts of the tree species that accounted for >1% of the diet of the two species suggests that the langurs at Kaludiyapokuna were not indiscriminate foragers feeding exclusively on the most common plant species but rather selective foragers that fed on a number of relatively uncommon species. This pattern is probably due to variation in nutritional value that has been shown to exist between plant species in tropical forests (Chapman et al. 2003). Similar patterns of food selection have also been observed in other colobine species such as *Colobus guereza* (Fashing 2001), *Rhinopithecus bieti* (Grueter et al. 2009) and *Trachypithecus francoisi* (Zhou et al. 2006). In addition, the spatial patterns of the majority of the 10 most frequently utilized plant species by Groups A, B and *T. vetulus* showed a clumped distribution pattern (Table 3.11). The clumped distribution observed for many plant species in this study is the predominant spatial distribution pattern observed for many tree species in tropical forests (Condit et al. 2000). The substantial home range overlap between *T. vetulus* and *S. entellus* and their preference for relatively rare species with clumped spatial distributions and limited resources such as fruit and flowers enhances the possibility of interspecific (Schoener 1982) and within-group competition in these species (Wrangham 1980; van

Schaik 1989; Isbell 1991). However, more recently, alternative hypotheses such as the resource dispersion hypothesis (RDH) have been proposed as a mechanism to explain group living (Johnson et al. 2002). The RDH is a hypothetical model that proposes that individuals can exploit patchy resources and satisfy their needs without imposing large costs on each other.

The study of *T. vetulus* and *S. entellus* at Kaludiyapokuna demonstrates that the species exhibit dietary plasticity across their geographic range and over time at a single study site in relation to resource availability. The feeding ecology of *T. vetulus* and *S. entellus* at Kaludiyapokuna differed from that reported in other published studies on the species in the langurs’ preferences for fruit and flowers even when immature leaves were abundant. In addition, both species preferred relatively rare plant species with clumped spatial distributions. Considering these factors, the general statement that Asian colobines subsist primarily on leaves is an oversimplification of the dietary ecology of these two species.

3.5 References

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3.6 Tables

Table 3.1. Composition of study groups. AM= Adult male, AF= Adult female, SA= Subadult, JV= Juvenile, IN = Infant.

Species	AM	AF	SA	JV	IN	Total
S. entellus						
Group A	3	7	3	7	2	22
Group B	2	5	1	4	1	13
T. vetulus	1	6	0	0	4	11

Table 3.2.Tree composition in the home ranges of the three groups.

	Group A (*S. entellus*)		Group B (*S. entellus*)		Group C (*T. vetulus*)	
Area sampled (ha)	1		0.52		0.48	
Number of species	48		37		30	
Number of families	24		19		19	
Stem density (stems/ha)	643		675		698	
DBH						
Mean (95% CI)	24.3 (22.5 26.1)		25.3 (22.6 28.0)		22.0 (20.0 24.0)	
Mode	9.0		10.5		9.0	
The 20 highest-ranking trees	Family	Species (BA/ha, relative BA/ha)	Family	Species (BA/ha, relative BA/ha)	Family	Species (BA/ha, relative BA/ha)
	Ulmaceae	*Holoptelea integrifolia* (83968, 15.1)	Moraceae	*Ficus microcarpa* (117702, 17.4)	Euphorbiaceae	*Drypetes sepiaria* (91747, 20.5)
	Euphorbiaceae	*Drypetes sepiaria* (76309, 13.7)	Moraceae	*Ficus amplissima* (79088, 11.7)	Moraceae	*Ficus microcarpa* (61443, 13.8)
	Moraceae	*Ficus microcarpa* (74749, 13.4)	Ulmaceae	*Holoptelea integrifolia* (70734, 10.5)	Flacourtiaceae	*Hydnocarpus venenata* (51509, 11.5)
	Euphorbiaceae	*Mischodon zeylanicus* (35250, 6.3)	Sterculiaceae	*Pterygota thwaitesii* (63050, 9.3)	Euphorbiaceae	*Mischodon zeylanicus* (49218, 11.0)
	Flacourtiaceae	*Hydnocarpus venenata* (34182, 6.1)	Sterculiaceae	*Pterospermum suberifolium* (39400, 5.8)	Datiscaceae	*Tetrameles nudiflora* (23571, 5.3)
	Sterculiaceae	*Pterospermum suberifolium* (29648,5.3)	Euphorbiaceae	*Drypetes sepiaria* (39226, 5.8)	Ebenaceae	*Diospyros ebenum* (22982, 5.1)
	Annonaceae	*Diospyros oocarpa* (24023, 4.3)	Ebenaceae	*Diospyros oocarpa* (37129, 5.5)	Sterculiaceae	*Pterospermum suberifolium* (20978, 4.7)
	Datiscaceae	*Terameles nudiflora* (22628 4.0)	Euphorbiaceae	*Mischodon zeylanicus* (27530, 4.1)	Sapindaceae	*Lepisanthes senegalensis* (14940, 3.3)
	Ebenaceae	*Diospyros ebenum* (14908, 2.7)	Lauraceae	*Cryptocarya sp.* (23035, 3.4)	Fabaceae	*Dialium ovoideum* (13801, 3.1)
	Annonaceae	*Xylopia nigricans* (13477, 2.4)	Sapindaceae	*Dimocarpus longan* (19981, 2.9)	Annonaceae	*Xylopia nigricans* (13718, 3.1)
	Lauraceae	*Cryptocarya sp.* (12019, 2.2)	Verbenaceae	*Vitex altissima* (16792, 2.5)	Ebenaceae	*Diospyros oocarpa* (13101, 2.9)
	Sapotaceae	*Manilkara hexandra* (11615, 2.1)	Annonaceae	*Xylopia nigicans* (15242, 2.2)	Tiliaceae	*Grewia rothii* (10248, 2.3)
	Aponogetonaceae	*Wrightia angustifolia* (10333, 1.8)	Euphorbiaceae	*Dimorphocalyx glabellus* (12244, 1.8)	Anacardiaceae	*Spondius dulcis* (8090, 1.8)
	Sapindaceae	*Lepisanthes senegalensis* (9518, 1.7)	Fabaceae	*Dialium ovoideum* (12064, 1.8)	Ebenaceae	*Diospyros ovalifolia* (7820, 1.8)
	Fabaceae	*Dialium ovoideum* (9448, 1.7)	Ebenaceae	*Diospyros ebenum* (11710, 1.7)	Lauraceae	*Cryptocarya sp.* (5519, 1.2)
	Tiliaceae	*Grewia rothii* (8739, 1.6)	Tiliaceae	*Grewia rothii* (9438, 1.4)	Ulmaceae	*Holoptelea integrifolia* (5115, 1.1)
	Sterculiaceae	*Pterygota thwaitesii* (8128, 1.4)	Clusiaceae	*Mesua ferrea* (9294, 1.4)	Sapindaceae	*Dimocarpus longan* (4801, 1.1)
	Euphorbiaceae	*Dimorphocalyx glabellus* (7117, 1.3)	Datiscaceae	*Tetrameles nudiflora* (7073, 1.0)	Sapindaceae	*Lepisanthes tetraphyla* (4644, 1.0)
	Sapindaceae	*Dimocarpus longan* (6718, 1.2)	Aponogetonaceae	*Wrightia flavido-rosea* (7007, 1.0)	Aponogetonaceae	*Wrightia angustifolia* (4519, 1.0)
	Verbenaceae	*Vitex altissima* (6708, 1.2)	Annonaceae	*Polyalthia coffeoides* (6989, 1.0)	Aponogetonaceae	*Wrightia tomentosa* (3169, 0.7)

Table 3.3. Percentage of time spent feeding overall and dietary item by *S. entellus* (Groups A and B) and *T. vetulus*.

	Group A (*S. entellus*) (n = 22)	Group B (*S. entellus*) (n = 13)	*T. vetulus* (n = 11)
Number of feeding records	4632	4725	1483
% of time spent feeding	33.62	19.88	13.94
Plant part			
Fruit (Whole fruit + seeds)	23.02	29.14	25.89
Whole fruit	14.57	17.71	19.55
Seeds	8.44	11.43	6.34
Flowers	23.94	13.42	11.33
Immature leaves	43.91	55.26	58.06
Mature leaves	8.72	2.18	4.72
Other			
Sap	0.39	0.00	0.00
Soil	0.02	0.00	0.00

Table 3.4. Percent monthly plant part consumption by *S. entellus* (Groups A and B) and *T. vetulus*.

Species	Month	Fruit	Whole fruit	Seeds	Flowers	Immature leaves	Mature leaves	Other
S. entellus	7/08	15.1	10.5	4.7	60.0	20.4	4.8	0.0
(Group A)	8/08	25.5	10.2	15.3	36.8	35.3	1.1	1.3
	9/08	15.1	11.2	4.0	24.6	60.0	0.0	0.2
	10/08	24.4	5.2	19.2	35.1	34.3	6.0	0.2
	11/08	41.5	17.5	24.0	0.2	35.7	22.0	0.8
	12/08	21.2	21.2	0.0	0.3	62.6	15.6	0.3
	1/09	42.2	42.2	0.0	1.0	40.5	16.0	0.3
	2/09	17.3	17.3	0.0	36.3	28.2	17.7	0.4
	3/09	2.0	2.0	0.0	30.6	63.0	4.6	0.0
	4/09	19.7	2.3	17.4	13.7	64.5	1.3	0.7
	5/09	4.7	4.7	0.0	0.0	91.0	4.2	0.0
	6/09	58.7	58.7	0.0	0.0	31.4	10.0	0.0
S. entellus	7/08	31.6	15.6	16.0	23.3	45.0	0.1	0.0
(Group B)	8/08	55.6	30.8	24.8	26.5	16.7	1.2	0.0
	9/08	43.6	18.8	25.0	7.8	48.6	0.0	0.0
	10/08	38.7	7.7	31.0	11.8	49.5	0.0	0.0
	11/08	15.1	12.4	2.7	11.4	73.5	0.0	0.0
	12/08	0.80	0.0	0.8	0.8	97.0	1.3	0.0
	1/09	0.0	0.0	0.0	0.0	92.2	7.8	0.0
	2/09	1.7	1.1	0.6	0.6	74.1	23.6	0.0
	3/09	6.2	6.2	0.0	13.0	75.1	5.8	0.0
	4/09	11.2	11.2	0.0	11.0	77.5	0.4	0.0
	5/09	26.1	26.1	0.0	8.8	65.1	0.0	0.0
	6/09	69.0	62.4	6.6	0.0	31.0	0.0	0.0
T. vetulus	7/08	46.1	46.1	0.0	10.5	43.4	0.0	0.0
(Group C)	8/08	47.1	14.2	32.9	27.3	20.4	5.2	0.0
	9/08	20.2	19.6	0.6	27.6	52.1	0.0	0.0
	10/08	26.4	25.3	1.1	14.7	58.9	0.0	0.0
	11/08	10.2	10.2	0.0	0.0	89.8	0.0	0.0
	12/08	24.6	24.6	0.0	0.0	75.4	0.0	0.0
	1/09	11.2	11.2	0.0	0.0	86.7	2.0	0.0
	2/09	10.4	10.4	0.0	0.0	56.5	33.1	0.0
	3/09	0.0	0.0	0.0	13.2	86.8	0.0	0.0
	4/09	8.0	8.0	0.0	6.8	85.2	0.0	0.0
	5/09	39.0	39.0	0.0	0.0	61.0	0.0	0.0
	6/09	78.2	78.2	0.0	0.0	18.2	3.6	0.0

Table 3.5.A. Percent of time spent feeding on food items by plant species (n = 4632) by Group A between July 2008 and June 2009.

Species	Family	Whole Fruit	Seeds	Flowers	Immature Leaves	Mature Leaves	Sap	Total
Drypetes sepiaria	Euphorbiaceae	2.05		5.48	4.36	0.10		12.00
Mischodon zeylanicus	Euphorbiaceae		0.28	0.02	9.09			9.39
Tetrameles nudiflora	Datiscaceae			4.43	4.62	0.02		9.07
Holoptelea integrifolia	Ulmaceae	0.56		6.74		1.30		8.59
Grewia rothii	Tiliaceae	4.21		1.19	1.84			7.23
Vitex altissima	Verbenaceae	2.53			4.40	0.02		6.95
Ficus microcarpa	Moraceae	0.73			4.17	0.02		4.92
Hydnocarpus venenata	Flacourtiaceae		4.21	0.50	0.19			4.90
Wrightia angustifolia	Aponogetonaceae	0.13		1.86	0.32	1.71		4.02
Manilkara hexandra	Sapotaceae			0.06	1.81	1.12		3.00
Lepisanthus senagalensis	Sapindaceae		1.12	0.09	1.73			2.94
Diospyros oocarpa	Ebenaceae		2.83					2.83
Combretum ovalifolia	Combretaceae	0.13		0.13	2.09			2.35
Cryptocarya sp.	Lauraceae				2.05			2.05
Lannea coromandelica	Anacardiaceae			1.55	0.04	0.30		1.90
Dialium ovoideum	Fabaceae	0.99			0.67			1.66
Diospyros ebenum	Ebenaceae					1.38		1.38
Glycosmis pentaphylla	Rutaceae			0.76	0.04	0.54		1.34
Commiphora caudata	Burseraceae				0.11	1.04		1.14
Democarpus longan	Sapindaceae	0.24		0.06	0.58			0.89
Sapuim sp.	Euphorbiaceae					0.71		0.71
Entada pusaetha	Fabaceae			0.15	0.52			0.67
Nothopegia beddomei	Anacardiaceae	0.63			0.04			0.67
Diospyros ovalifolia	Ebenaceae					0.56		0.56
Macaranga peltata	Euphorbiaceae	0.56						0.56
Tricalysia dalzelli	Rubiaceae	0.35			0.04	0.15		0.54
Xylopia nigricans	Annonaceae			0.41	0.06			0.47
Ficus amplissima	Moraceae	0.28			0.15	0.02		0.45
Bauhinia tomentosa	Fabaceae				0.41			0.41
Memecylon sylvaticum	Melastomataceae	0.39						0.39
Schefflera emarginata	Arecaceae						0.39	0.39
Mikania scandens	Asteraceae				0.37			0.37
Mallotus eriocarpus	Euphorbiaceae	0.13		0.17	0.04			0.35
Ochna lanceolata	Ochnaceae				0.32			0.32

(*Continued*)

Table 3.5.A. (*Continued*)

Species	Family	Whole Fruit	Seeds	Flowers	Immature Leaves	Mature Leaves	Sap	Total
Stereospermum colais	Bignoniaceae				0.30			0.30
Lepisanthes tetraphylla	Sapindaceae				0.28			0.28
Pterospermum suberifolium	Sterculiaceae	0.19		0.04	0.02			0.26
Schleichera oleosa	Sapindaceae				0.26			0.26
Spondias dulcis	Anacardiaceae					0.26		0.26
Basilicum polystachyon	Lamiaceae				0.22	0.02		0.24
Ficus racemosa	Moraceae	0.24						0.24
Diopyros malabarica	Ebenaceae				0.19			0.19
Carissa inermis	Apocynaceae	0.13						0.13
Hugonia ferruginea	Linaceae				0.13			0.13
Opilia amentacea	Opiliaceae			0.02	0.11			0.13
Canthium coromandelicum	Rubiaceae				0.02	0.09		0.11
Ixora pavetta	Rubiaceae					0.09		0.09
Premna procumbens	Verbenaceae			0.06	0.02			0.09
Broussonetia zeylanica	Moraceae				0.06			0.06
Hibiscus eriocarpus	Malvaceae			0.06				0.06
Abelmoschus angulosus	Malvaceae				0.04			0.04
Flueggea leucopyrus	Euphorbiaceae				0.04			0.04
Mallotus phillipiensis	Euphorbiaceae	0.04						0.04
Pterygota thwaitesii	Sterculiaceae				0.04			0.04
Ventilago madraspatana	Rhamnaceae	0.04						0.04
Carmona retusa	Boraginaceae					0.02		0.02
Unidentified liana					1.08	0.04		1.12

Table 3.5.B. Percent of time spent feeding on food items by plant species (n = 4725) by Group B between July 2008 and June 2009.

Species	Family	Whole Fruit	Seeds	Flowers	Immature Leaves	Mature Leaves	Sap	Total
Mischodon zeylanicus	Euphorbiaceae		3.34	0.17	19.58			23.09
Tetrameles nudiflora	Datiscaceae	0.06		5.63	4.00	0.36		10.05
Hydnocarpus venenata	Flacourtiaceae		5.88	0.28	0.49			6.65
Macaranga peltata	Euphorbiaceae	5.93		0.13	0.36			6.41
Drypetes sepiaria	Euphorbiaceae	4.30			0.59			4.89
Vitex altissima	Verbenaceae	0.21		0.97	3.11	0.53		4.83
Mikania scandens	Asteraceae				4.72			4.72
Grewia rothii	Tiliaceae	0.04		0.04	3.56	0.42		4.06
Dialium ovoideum	Fabaceae	2.35		0.08	1.61			4.04
Pterospermum suberifolium	Sterculiaceae	0.97		0.42	2.43			3.83
Ficus microcarpa	Moraceae	1.90			0.99			2.90
Premna procumbens	Verbenaceae	0.19		2.10	0.47			2.75
Combretum ovalifolia	Combretaceae			0.49	2.10			2.58
Democarpus longan	Sapindaceae	0.02		0.08	2.35	0.02		2.48
Entada pusaetha	Fabaceae			0.42	2.05			2.48
Ficus amplissima	Moraceae	0.42			1.97			2.39
Pterygota thwaitesii	Sterculiaceae		0.70	0.08	1.35			2.14
Diospyros oocarpa	Ebenaceae		1.74					1.74
Mallotus eriocarpus	Euphorbiaceae			1.59	0.15			1.74
Cryptocarya sp.	Lauraceae				1.23			1.23
Wrightia angustifolia	Aponogetonaceae			0.11	0.66	0.23		0.99
Ficus virens	Moraceae	0.97						0.97
Bridelia retusa	Euphorbiaceae				0.66			0.66
Wrightia flavido-rosea	Aponogetonaceae			0.49				0.49
Tiliacora acuminata	Menispermaceae				0.11	0.32		0.42
Holoptelea integrifolia	Ulmaceae	0.11				0.30		0.40
Polyalthia coffioides	Annonaceae				0.28			0.28
Bauhinia tomentosa	Fabaceae							0.23
Xylopia nigricans	Annonaceae			0.19				0.19
Glycosmis pentaphylla	Rutaceae			0.15				0.15
Lepisanthes tetraphylla	Sapindaceae				0.15			0.15
Limonia acidissima	Rutaceae				0.08			0.08

Table 3.5.C. Percent of time spent feeding on food items by plant species (n = 1483) by *T. vetulus* between July 2008 and June 2009.

Species	Family	Whole Fruit	Seeds	Flowers	Immature Leaves	Mature Leaves	Sap	Total
Ficus microcarpa	Moraceae	6.20			9.37			15.58
Mischodon zeylanicus	Euphorbiaceae				12.00			12.00
Commiphora caudata	Burseraceae	0.07		0.07	6.00	2.29		8.43
Tetrameles nudiflora	Datiscaceae			4.79	4.38			9.17
Drypetes sepiaria	Euphorbiaceae	1.89			4.59			6.47
Diospyros oocarpa	Ebenaceae		6.34					6.34
Combretum ovalifolia	Combretaceae	2.49		0.81	1.89			5.19
Dialium ovoideum	Fabaceae	2.29			2.23			4.52
Ficus arnottiana	Moraceae	0.67			3.71			4.38
Wrightia angustifolia	Aponogetonaceae	0.13		1.48	0.88	1.08		3.57
Democarpus longan	Sapindaceae				2.97			2.97
Manilkara hexandra	Sapotaceae				2.36	1.01		3.37
Lannea coromandelica	Anacardiaceae			1.35	0.61	0.20		2.16
Opilia amentacea	Opiliaceae				1.96			1.96
Holoptelea integrifolia	Ulmaceae			1.75	0.13			1.89
Tricalysia dalzelli	Rubiaceae	0.54			0.81	0.13		1.48
Pterospermum suberifolium	Sterculiaceae	1.35			0.07			1.42
Grewia rothii	Tiliaceae	0.81			0.40			1.21
Memecylon sylvaticum	Melastomataceae	1.21						1.21
Xylopia nigricans	Annonaceae				1.08			1.08
Mallotus eriocarpus	Euphorbiaceae			0.81	0.20			1.01
Vitex altissima	Verbenaceae	0.47			0.24			0.78
Ficus mollis	Moraceae	0.27			0.34			0.61
Ixora pavetta	Rubiaceae	0.34						0.34
Hydnocarpus venenata	Flacourtiaceae		0.27					0.27
Lepisanthes tetraphylla	Sapindaceae				0.27			0.27
Spondias dulcis	Anacardiaceae				0.27			0.27
Entada pusaetha	Fabaceae				0.20			0.20
Abelmoschus angulosus	Malvaceae				0.20			0.20
Glycosmis pentaphylla	Rutaceae			0.20				0.20
Lepisanthes senegalensis	Sapindaceae			0.07				0.07
Unidentified species 1	Unidentified				0.07			0.07
Unidentified species 2	Unidentified				0.40			0.40
Unidentified species 3	Unidentified	0.81						0.81

Table 3.6. Spearman correlation coefficient (r_s) values for monthly consumption of different plant items *versus* their availability in Groups A and B and *T. vetulus* from July 2008 to June 2009. * = $p \leq 0.05$; ** = $p \leq 0.01$

Group	% Fruit in diet vs monthly FAI fruit	% Flowers in diet vs monthly FAI flowers	% Immature leaves in diet vs monthly FAI immature leaves
S. entellus (A)	0.629*	0.889**	0.441
S. entellus (B)	0.671*	0.790**	-0.238
T. vetulus (C)	0.762*	0.694**	-0.315

Table 3.7. Spearman correlation coefficient (r_s) values for monthly total leaf consumption versus the availability of fruits and flowers and the monthly mature leaf consumption versus immature leaf availability in Groups A and B and *T. vetulus* from July 2008 to June 2009. * = $p \leq 0.05$; ** = $p \leq 0.01$

Group	% Leaves in diet vs monthly FAI fruit	% Leaves in diet vs monthly FAI flowers	% Mature leaves in diet vs monthly FAI immature
S. entellus (A)	-0.517	-0.479	-0.741**
S. entellus (B)	-0.650*	-0.401	-0.276
T. vetulus (C)	-0.601*	-0.238	-0.391

Table 3.8. Forage ratios for different plant parts of species accounting for ≥ 1% of the annual diet of *S. entellus* Group A and B. Fr = Fruit; Fl = Flowers; Iml = Immature leaves; Mal = Mature leaves; % of diet = % of annual diet; * = plant part selected; ** = plant species selected; - = plant parts that not consumed; D/N/A = shrub species or not in the vegetation plots.

		S.entellus group A						*S.entellus* group B			
			w_i						w_i		
Species	Fr	Fl	Iml	Mal	% of diet	Species	Fr	Fl	Iml	Mal	% of diet
Drypetes sepiaria	0.27	0.71	0.57	0.01	12.00	*Mischodon zeylanicus*	0.23	0.01	1.33*	-	23.09**
Mischodon zeylanicus	0.02	0.00	0.62	-	9.39	*Tetrameles nudiflora*	0.12	11.06*	7.85*	0.71	10.05**
Tetrameles nudiflora	-	8.70*	9.07*	0.04	9.07**	*Hydnocarpus venenata*	5.77*	0.27	0.48	-	6.65**
Holoptelea integrifolia	4.03*	48.53*	-	9.36*	8.59**	*Macaranga peltata*	32.02*	0.70	1.94*	-	6.41**
Grewia rothii	1.26*	0.36	0.55	-	7.23**	*Drypetes sepiaria*	0.56	-	0.08	-	4.89
Vitex altissima	6.07*	-	10.56*	0.05	6.95**	*Vitex altissima*	0.50	2.33*	7.46*	1.27*	4.83**
Ficus microcarpa	1.21*	-	6.93*	0.03	4.92**	*Mikania scandens*	D/N/A	D/N/A	D/N/A	D/N/A	4.72
Hydnocarpus venenata	4.13*	0.49	0.19	-	4.90**	*Grewia rothii*	0.01	0.01	1.07*	0.13	4.06**
Wrightia angustifolia	0.11	1.55*	0.27	1.42*	4.02**	*Dialium ovoideum*	2.99*	0.10	2.05*	0.00	4.04**
Manilkara hexandra	-	0.32	9.77*	6.05*	3.00**	*Pterospermum suberifolium*	0.37	0.16	0.92	-	3.83
Lepisanthus senagalensis	0.18	0.01	0.27	-	2.94	*Ficus microcarpa*	3.16*	-	1.64*	-	2.90**
Diospyros oocarpa	0.29	-	-	-	2.83	*Premna procumbens*	0.82	9.07*	2.03*	-	2.75**
Combretum ovalifolia	0.18	0.18	2.82*	-	2.35**	*Combretum ovalifolia*	0.66	2.83*	-	-	2.58**
Cryptocarya sp.	-	-	0.52	-	2.05	*Dimocarpus longan*	0.01	0.03	0.91	0.01	2.48
Lannea coromandelica	-	8.37*	0.22	1.62*	1.90**	*Entada pusaetha*	0.00	1.13*	5.53*	-	2.48**
Dialium ovoideum	1.26*	-	0.85	-	2.11**	*Ficus amplissima*	2.27*	-	10.64*	-	2.39**
Diospyros ebenum	-	-	-	9.15*	1.38**	*Pterygota thwaitesii*	2.16*	0.25	4.17*	-	2.14**
Glycosmis pentaphylla	D/N/A	D/N/A	D/N/A	D/N/A	1.34	*Diospyros oocarpa*	0.18	-	-	-	1.74
Commiphora caudata	-	-	0.97	9.15*	1.14**	*Mallotus eriocarpus*	-	0.19	0.02	-	1.74
Unidentified liana	D/N/A	D/N/A	D/N/A	D/N/A	1.12	*Cryptocarya* sp.	-	-	0.31	-	1.23

Table 3.9. Forage ratios for different plant parts of species accounting for ≥ 1% of the annual diet of *T. vetulus*. Fr = Fruit; Fl = Flowers; Iml = Immature leaves; Mal = Mature leaves; % of diet = % of annual diet; * = plant part selected; ** = plant species selected; - = plant parts that not consumed; D/N/A = shrub species or not in the vegetation plots.

		T. vetulus			
			w_i		
Species	Fr	Fl	Iml	Mal	% of diet
Ficus microcarpa	10.16*	-	15.35*	-	15.58**
Mischodon zeylanicus	-	-	0.81	-	12.00
Tetrameles nudiflora	-	9.27*	8.48*	-	9.17**
Commiphora caudata	0.48	0.48	42.56*	16.26*	8.43**
Drypetes sepiaria	0.24	-	0.59	-	6.47
Diospyros oocarpa	0.62	-	0.01	-	6.34
Combretum ovalifolia	3.32*	1.08*	2.51*	-	5.19**
Dialium ovoideum	2.87*	-	2.79*	-	4.52**
Ficus arnottiana	11.48*	-	53.12*	-	4.38**
Wrightia angustifolia	0.11	1.21*	0.72	0.88*	3.57**
Manilkara hexandra	-	-	12.56*	5.38*	3.37**
Democarpus longan	-	-	1.13*	-	2.97**
Lannea coromandelica	-	7.18*	3.23*	1.08*	2.16**
Opilia amentacea	-	-	12.26*	-	1.96**
Holoptelea integrifolia	-	12.44*	0.96	-	1.89**
Tricalysia dalzelli	0.30	-	0.45	0.08	1.48
Pterospermum suberifolium	0.50	0.00	0.00	0.03	1.42
Grewia rothii	0.24	-	0.12	-	1.21
Memecylon sylvaticum	D/N/A	D/N/A	D/N/A	D/N/A	1.21
Xylopia nigricans	-	-	0.55		1.08
Mallotus eriocarpus	-	0.19	0.05	-	1.01

Table 3.10. Dietary comparison (%) among *S. entellus*, *T. vetulus* and other African and Asian colobine species.

Species	Fruit	Seeds	TotFr	Flowers	Leaves	Other	No. species	Study site	Reference
Colobus guereza (1)	42.6	1.4	44.0	0.7	48.1	8.5	28+	Kakamega Kenya	Fashing (2001)
Colobus guereza (2)	32.1	1.0	33.1	0.2	57.4	12.7	28+	Kakamega Kenya	Fashing (2001)
Colobus angolensis	17	50	67	6	27	-	46	Salonga, D.R. Congo	Maisels et al. (1994)
Colobus satanas	0.0	53.2	53.2	3.3	38.6	4.9	56	Douala-Edea, Cameroon	McKey et al. (1981)
Procolobus badius	4.2	1.4	5.8	15.9	73.4	5.1	57	Kibale, Uganda	Strusaker (1978)
Procolobus badius	7.1	30.8	37.9	1.4	60.7	0.0	84	Salonga, D.R. Congo	Maisels et al. (1994)
Procolobus badius	6	25	31	16	52	1.0	-	Tiwai, Sierra Leone	Davies et al. (1999)
Trachypithecus pileatus	24.4	9.3	33.7	7.0	57.8	1.5	35	Madhupur, Bangladesh	Stanford (1991)
Trachypithecus pileatus	-	-	16	16	68	-	52	Pakhui. India	Solanki et al. (2008)
Trachypithecus johnii	-	-	25.1	9.3	62.2	3.4	107+	Kakachi, India	Oates et al. (1980)
Trachypithecus phayrei	-	-	14	16	70	0	29	Lawachara, Bangladesh	Aziz & Feeroz (2009)
Trachpithecus delacouri	-	-	9	5	80	6	42	Van Long, Vietnam	Workman (2010)
Trachypithecus leucocephalus	5.7	0.4	6.1	2.7	91.2	-	50	Fusui, China	Li & Rogers (2006)
Trachypihecus francoisi	-	-	3.1	0.5	94.5	2.0	37	Fusui, China	Huang et al (2008)
Trachypihecus francoisi	17.2	14.2	31.4	7.5	52.8	8.4	90	Nonggang, China	Zhou et al. (2006)
Trachypithecus vetulus	-	-	28	12	60	0	-	Polonnaruwa, Sri Lanka	Hladik (1977)
Trachypithecus vetulus (1)	52.3	1.4	53.7	7.6	31.7	-	-	Panadura, Sri Lanka	Dela (2007)
Trachypithecus vetulus (2)	53.9	6.2	60.1	4.0	29.4	-	-	Piliyandala, Sri Lanka	Dela (2007)
Trachypithecus vetulus	19.5	6.3	25.8	11.3	62.8	0.0	31+	Kaludiyapokuna, Sri Lanka	this study
Semnopithecus entellus (P 91/92)	-	-	15.1	6.3	59.8	3.1	-	Ramnagar, India	Koenig & Borries (2001)
Semnopithecus entellus (P 92/93)	-	-	21.9	12.8	52.4	3.8	-	Ramnagar, India	Koenig & Borries (2001)
Semnopithecus entellus (O)	-	-	23.2	4.4	60.9	0.4	-	Ramnagar India	Koenig & Borries (2001)
Semnopithecus entellus	-	-	24.4	9.5	51.6	14.5	53	Kanha, India	Newton (1992)
Semnopithecus entellus	-	-	21.0	6.8	56.8	15.4	43	Langtang, Nepal	Sayers & Norconk (2008)
Semnopithecus entellus	-	-	45	7	48	0	-	Polonnaruwa, Sri Lanka	Hladik (1977)
Semnopithecus entellus (A)	14.6	8.4	23.0	23.9	52.6	0.4	58	Kaludiyapokuna, Sri Lanka	this study
Semnopithecus entellus (B)	17.7	11.4	29.1	13.4	57.4	-	32	Kaludiyapokuna, Sri Lanka	this study
Presbytis rubucunda	-	-	49.6	11.1	37.6	2.0	103+	Sepilok, Malaysia	Davies (1991)
Presbytis potenziani	-	-	32	-	55	13	42	Betumonga, North Pagai	Fuentes (1996)
Presbytis melalophos	-	-	56	6	35	2	137	Kuala Lompat, Malaysia	Curtin (1980)
Rhinopithecus roxellana	-	-	29.4	-	24	46.6	84+	Zhouzhi, China	Guo et al. (2007)
Pygathrix nigripes	-	-	31.6	12.4	54.4	1.6	-	Nui Chua, Vietnam	Hoang et al. (2009)
Pygathrix nigripes	-	-	27.4	16.4	54.8	1.4	-	Phuoc Binh, Vietnam	Hoang et al. (2009)
Nasalis larvatus	-	-	40.3	3.0	51.9	4.8	47	Tanjung Puting, Indonesia	Yearger (1989)

Table 3.11. Spatial distribution of the top 10 most frequently utilized plant species by Groups A, B and *T. vetulus* during the study period. n = number of individuals in the sample; Rank = the rank of the species in relation to the relative density of 67 plant species in the sample § = species listed in 10 most frequently used food plant species by *T. vetulus*; * = species listed in 10 most frequently used food plant species by Group A; $^{\Delta}$ = species listed in 10 most frequently used food plant species by Group B.

Species	**n**	**Rank**	**(I_p)**	**(I_d) ($p \leq$)**	**Conclusion**
Commiphora caudata §	3	43	--------	--------	-----------$^{\#}$
Combretum ovalifolia §	16	22	0.552	8.358 (0.00)	Clumped
Dialium ovoideum $^{\Delta}$	17	21	-0.488	2.169 (0.06)	Random
Dimocarpus longan §	56	12	0.505	2.031 (0.00)	Clumped
Diospyros oocarpa §	214	2	0.506	1.742 (0.00)	Clumped
Drypetes sepiaria *$^{\Delta\S}$	166	5	0.507	1.995 (0.00)	Clumped
Ficus arnottiana §	1	58	--------	--------	-----------$^{\#}$
Ficus microcarpa *§	15	23	-0.045	1.124 (0.41)	Random
Grewia rothii *$^{\Delta}$	72	10	0.514	2.885 (0.00)	Clumped
Holoptelea integrifolia *	3	46	--------	--------	Clumped$^{\#}$
Hydnocarpus venenata *$^{\Delta}$	22	17	0.580	11.238 (0.00)	Clumped
Macaranga peltata $^{\Delta}$	4	38	--------	--------	-----------
Manilkara hexandra *	4	39	--------	--------	Clumped$^{\#}$
Mikania scandens $^{\Delta}$	-	-	--------	--------	-----------$^{\#}$
Mischodon zeylanicus *$^{\Delta\S}$	317	1	0.515	2.835 (0.00)	Clumped
Pterospermum suberifolium $^{\Delta}$	57	11	0.512	2.736 (0.00)	Clumped
Tetrameles nudiflora *$^{\Delta\S}$	11	28	0.567	10.727 (0.00)	Clumped
Vitex altissima *$^{\Delta}$	9	30	--------	--------	-----------$^{\#}$
Wrightia angustifolia *§	26	16	-0.414	1.634 (0.08)	Random

Morisita's index (I_d) assumes unity (1.0) for a random distribution, over 1.0 for a clumped distribution, and less than 1.0 for a uniform distribution. The Standardized Morisita Index (I_p) ranges from -1.0 to + 1.0, with 95% confidence intervals at ± 0.5. Random patterns give a value of zero, clumped patterns above zero and uniform patterns below zero. The null hypothesis of randomness was tested by computing a χ^2 statistic for index values. *Certain species were represented by small sample size and hence the computation of indices of dispersion was not possible. In some of these cases, conclusions on patterns of dispersion was based on a published study on a similar dry evergreen forest tree community in the north central dry zone of Sri Lanka (see Dittus 1977).

3.7 Figures

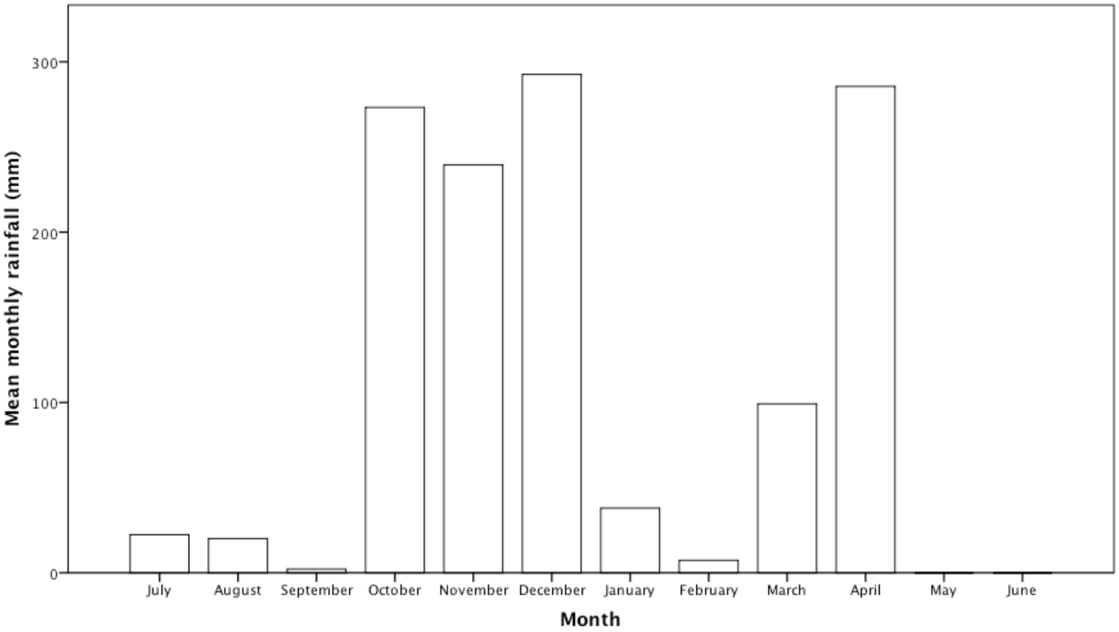

Figure 3.1. Rainfall pattern at Kaludiyapokuna during July 2008 to June 2009 showing peaks in October-December and March-April. Notably the driest months produced almost no rainfall.

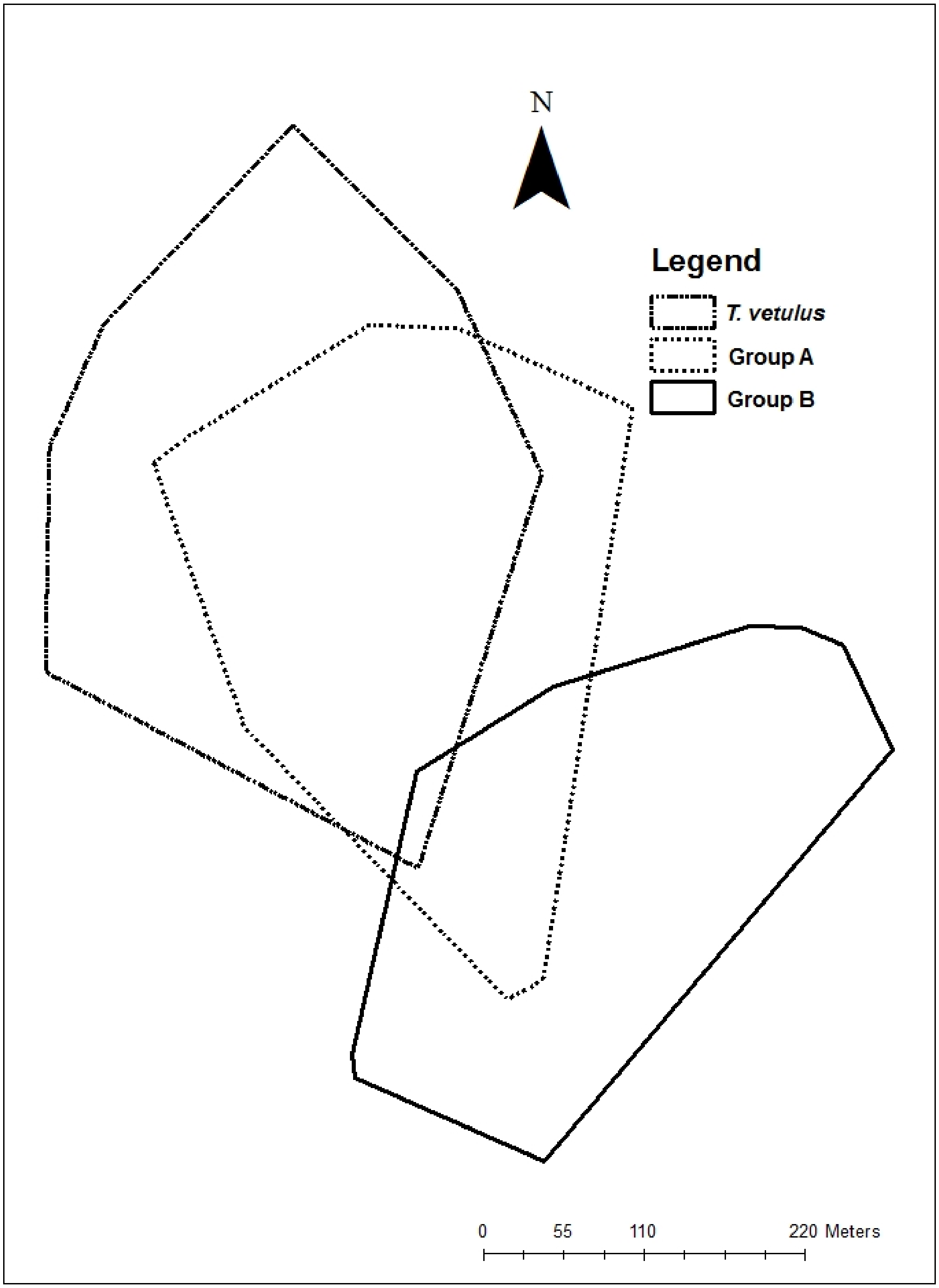

Figure 3.2. Home ranges of *T. vetulus* and Groups A and B.

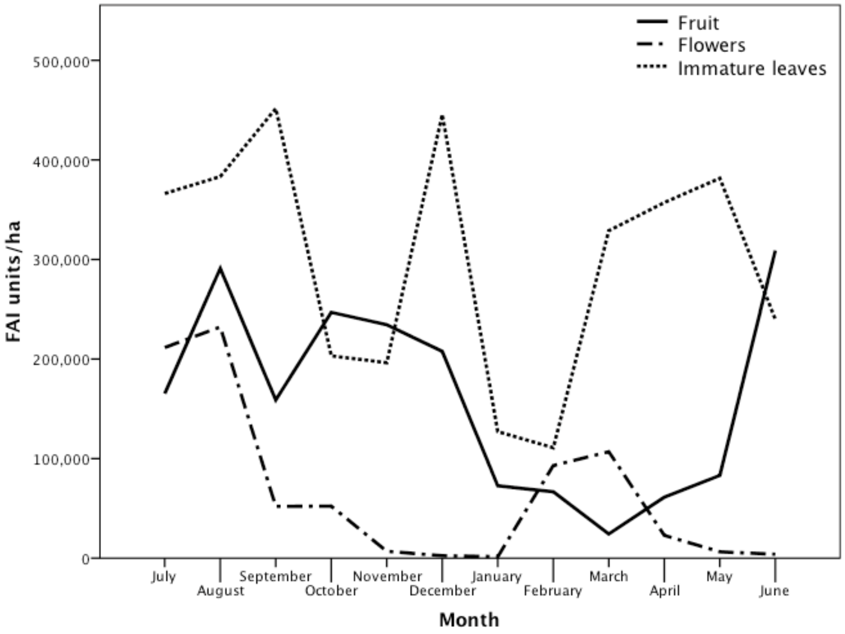

Figure 3.3. Monthly variation in fruit, flower and immature leaf availability in FAI units/ha in the study site from July 2008 to June 2009.

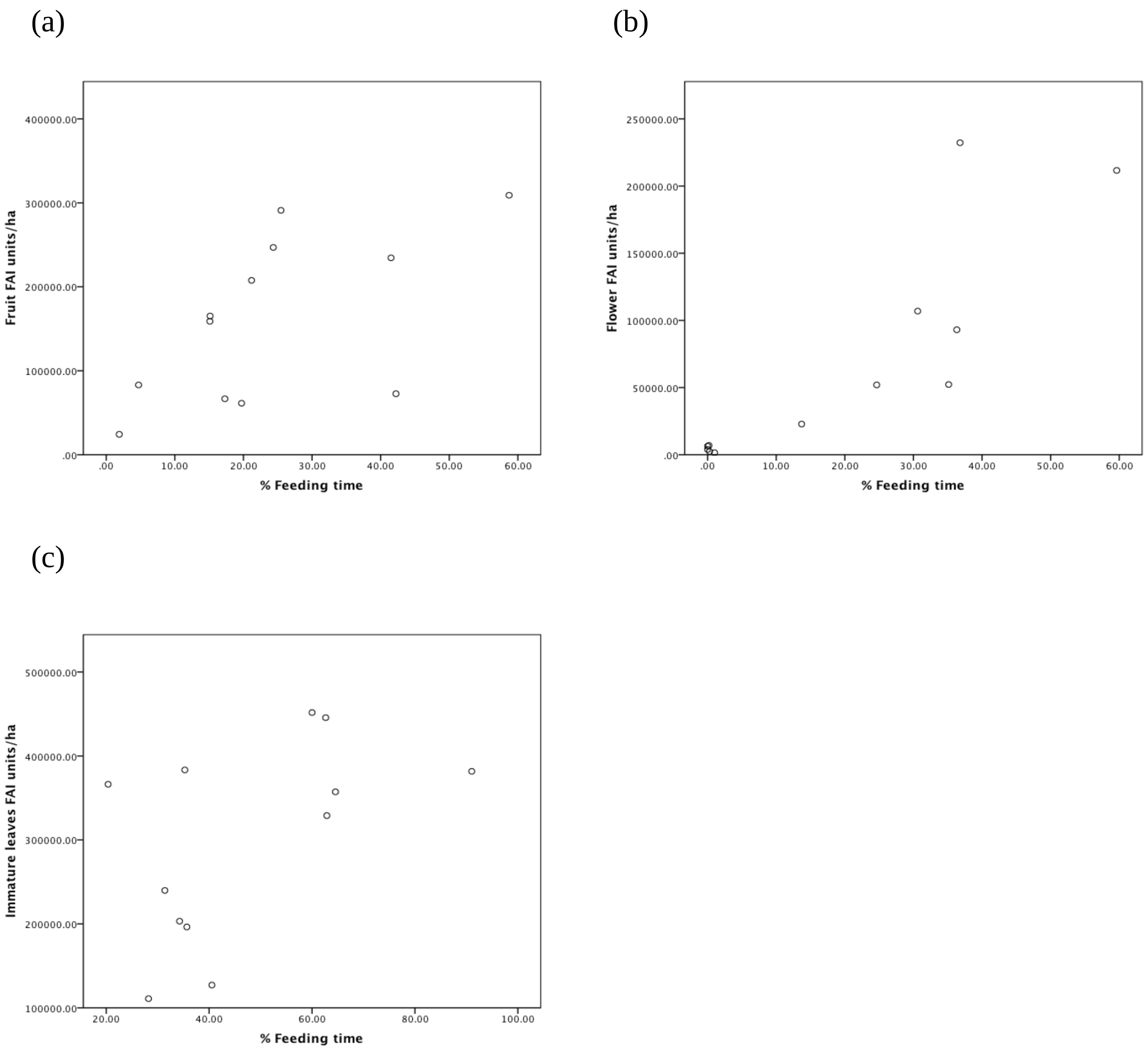

Figure 3.4. A visual representation of Spearman rank order correlations between monthly plant part availability *versus* monthly plant part consumption for *S. entellus* Group A. (a) Fruit availability vs % fruit in diet (r_s= 0.629*), (b) flower availability vs % flowers in diet (r_s= 0.889**) and (c) immature leaf availability vs % immature leaves in diet (r_s= 0.441). Similar patterns of plant part consumption in relation to plant part availability were observed in *S. entellus* Group B and *T. vetulus*. These figures illustrate a correlation; these are not a regression and there is no intention of predicting the values of one axis from those on the other. *= $p \leq 0.05$; **= $p \leq 0.01$

Chapter 4

Comparative ranging behavior of *Semnopithecus entellus* and *Trachypithecus vetulus* in the Kaludiyapokuna forest reserve

4.1 Introduction

A growing number of field studies have demonstrated a remarkable level of variation in the ranging behavior of primates. The spatial distribution and availability of resource have been identified as important factors influencing the ranging behavior of primates (Di Fiore 2003; Teichroeb and Sicotte 2009). In addition, other factors such the availability of resting places (Rasmussen 1979; Hamilton 1982), body size (Milton and May 1976; Terborgh 1983), weather (McKey and Waterman 1982; Olupot et al. 1997) and the probability of disease transmission (Freeland 1976; Hausfater and Meade 1982) have also been identified as factors influencing ranging behavior in primates.

Within a given species, home range size has been shown to increase with increases in group sizes (van Schaik et al. 1983; Teichroeb and Sicotte 2009). Similarly, interspecific home ranges have also been noted to increase with group biomasses (Milton and May 1976). In addition, in a number of primate species, daily path lengths have been shown to be influenced by group size and habitat quality. On average, larger groups have been reported to travel farther on a given day than smaller groups (e.g., *Macaca fascicularis* (van Schaik et al. 1983), *Theropithecus gelada* (Iwamoto and Dunbar 1983), *Presbytis thomasi* (Steenbeek and van Schaik 2001) and *Colobus vellerosus* (Teichroeb and Sicotte 2009)). Also groups living in habitats poor in food resources have been shown to travel farther on a given day in comparison with similar- sized groups living in high quality habitats (Struhsaker 1967). These observations have been interpreted as evidence for the notion that primates are food limited and the energetic demands of larger groups are greater than smaller groups (Chapman and Chapman 2000; Teichroeb and Sicotte 2009). This relationship between ranging behavior, primate group size and habitat quality is the foundation for the ecological constraints model, which hypothesizes that if food availability is held constant an increase in group size should lead to an increase in day-range length (Janson and Goldsmith 1995; Chapman and Chapman 2000; Teichroeb and Sicotte 2009). In situations where food availability remains constant, the increase in day-range length with group size has been identified as evidence for within-group scramble competition and has been identified as a factor influencing primate group size (Chapman and Chapman 2000; Gillespie and Chapman 2001). In addition, differences in ranging behaviors and niche partitioning between primates have also been used to explain the coexistence of sympatric species. In the case of sympatric populations of *S. entellus* and *T. vetulus*, it has been suggested that coexistence is facilitated by *S. entellus* ranging over a wide area in search of high energy food resources located in patches and *T. vetulus* adopting a less mobile system and feeding predominantly on leaves, which are low in nutritional gain and ubiquitous in the environment (Hladik 1977).

Despite these within-species and cross-species relationships between ranging behavior, habitat quality and group size, the relationships between these variables for the same local population over time is unclear as no consistent pattern has immerged from the studies that have explored this issue. For example, there was no relationship between food availability and mean day-range length in *Cercopithecus mitis* and *Cercopithecus lhoesti* (Kaplin 2001) but *Procolobus badius* was found to range farther during periods of food scarcity (Marsh 1981). A similar study found that *Hylobates lar* travelled shorter distances when food availability was low (Raemakers 1980). These results suggest that primates adopt different foraging strategies to cope with resource scarcity. Animals may choose to visit a greater number of food patches in search of food as food availability decreases, and this may result in longer daily path lengths. Conversely, animals may adopt a strategy for saving energy and reduce daily travel until conditions improve (Di Fiore 2003). Currently, our understanding of the relationships between group size, ranging behavior and food availability are predominantly based on studies conducted on frugivorous primates (reviewed in Chapman and Chapman 2000), and relatively few studies have explored these relationships in the context of foli-frugivorous primates such as colobines (Gillespie and Chapman 2001; Teichroeb and Sicotte 2009). Hence, the broader applicability of these relationships to colobine monkeys is yet to be determined.

This chapter focuses on the ranging behavior of sympatric *T. vetulus* and *S. entellus* living in an undisturbed dry zone forest in the north central dry zone of Sri Lanka. Much of what is known about the ecology of forest dwelling *S. entellus* and *T. vetulus* in Sri Lanka is from Polonnaruwa, a heavily disturbed secondary dry zone forest, where these primates occur sympatrically. These studies have focused on the social organization and reproduction of *T. vetulus* (Rudran 1973a; 1973b), social organization and general feeding ecology of *S. entellus* (Ripley 1965; 1967; 1970) and feeding behavior of sympatric *T. vetulus* and *S. entellus* in relation to phenology (Hladik 1977). In comparison, relatively little is known on the ranging behavior and the factors that influence ranging in these primates in Sri Lanka. This chapter specifically explores the relationship between daily path length and seasonal availability of fruit, flowers and immature leaves to determine, which of these foraging strategies characterizes this local population. In addition, this chapter aims to provide basic data on home range size, overlap and intensity of home range use. This knowledge may shed light on mechanisms that enable these primates to coexist. Finally, the chapter compares the ranging behavior of these primate species to other colobine species and populations studied elsewhere with the aim of broadening the understanding of the influence of food resource availability on the ranging behavior of colobine monkeys.

4.2 Material and methods

4.2.1 Study area

The study was conducted in the Kaludiyapokuna forest reserve (N 07° 52.5, E 080° 44.1) located in the Matale district in the north central dry zone of Sri Lanka. The study was conducted under the authority of the Department of Wildlife Conservation of Sri Lanka and in collaboration with the University of Peradeniya, Sri Lanka. The main study area is approximately 2.2 km^2 in extent and is contiguous with the Knuckles forest range in the south. The study site is surrounded by farmland and human settlements from the north, east and west. The study site is undisturbed by humans and the primates are not provisioned, unlike the Polonnaruwa study site, which is disturbed and where primates have become accustomed to humans through regular contact (Bishop et al. 1981). Also there is no evidence to indicate that hunting, timber extraction or woodcutting has occurred at the site. The study site supports populations of four species of primates, as well as populations of other herbivorous mammals such as Asian elephants (*Elephas maximus*), spotted deer (*Axis axis*), sambar deer (*Cervus unicolor*), and wild pig (*Sus scrofa*). Unlike Polonnaruwa (Bishop et al. 1981), this study area is home to a full complement of potential primate predators such as the black eagle (*Ictinaetus malayensis*), leopard (*Panthera pardus*) and python (*Python molurus*).

The study area receives about 1250 mm of rainfall annually and average temperature in the region ranges between 27-29 º C. The region receives most of its rainfall through convectional rains from October to November, which gradually grade into the northeast (NE) monsoon. The NE monsoon lasts from December to February and is most active during the month of December. The NE monsoon brings considerably less moisture than the southwestern (SW) monsoon, which lasts May to September. The northern dry zone is shielded from the SW monsoon rains by the central hills of the island and hence it experiences a characteristic period of drought during this time.

4.2.2 Subjects

In Sri Lanka, *S. entellus* is represented by the subspecies *S. entellus thersites* (Bennett and Davies 1994) and is found throughout the well-wooded areas of the entire dry zone from south of Jaffna, in the North, to the shores of the extreme southern coast (Phillips 1935). The purple-faced leaf monkey, *T. vetulus* is endemic to Sri Lanka and is divided into four distinct subspecies all occupying different geographic regions. *T. vetulus philbricki,* the northern dry zone subspecies, shares its range with *S. entellus.*

Dietary data were collected over a 12-month period between July 2008 and June 2009 as part of a long-term study on the comparative ecology of *T. vetulus* and *S. entellus* in Sri Lanka. Data collection was confined to two groups of *S. entellus* and one group of *T. vetulus*. At the time of data collection, all groups were habituated to human observers and could be approached to within a distance of 10 m without showing signs of alarm. The composition of the study groups was stable throughout the study period (Table 4.1).

Groups A and B were neighboring groups with overlapping home ranges. Similarly, Group A and *T. vetulus* were neighboring groups with overlapping home ranges. Group B and *T. vetulus* did not overlap in their home ranges.

4.2.3 Forest composition

Vegetation sampling was carried out using vegetation plots (Ganzhorn 2003). Localities for sampling were chosen with the aid of a WorldView 1 satellite image of the study area and care was taken to ensure that the localities were evenly distributed across the study area so that an unbiased representative sample of the vegetation of the study area could be obtained. Each plot was 20 x 20 m, and 59 plots were used to sample the vegetation at the study site. The trees that were greater than 9 cm in diameter at breast height (DBH) and all woody lianas were measured using a DBH tape. Plant samples were collected and herbarium sheets were prepared and the specimens were identified and compared to voucher specimens at the National Herbarium at the Royal Botanical Gardens, Peradeniya, Sri Lanka. The basal area (BA) for each tree was calculated using the formula:

$$BA = [0.5 \times DBH]^2 \times \pi.$$

The measure BA per hectare was as used to define the biomass of each plant species within the home range of each group (Fashing 2001).

4.2.4 Forest phenology

To produce a quantitative measure of food availability, 958 trees and lianas in 22 phenological plots were monitored each month for phenological activity. The plant species monitored included species that were consumed by the primates as well as species that were not consumed by the primates. Phenological assessment of trees was carried out with the help of two field assistants during the first week of each month. The crown of each tree was scanned by the investigator and the two field assistants with the aid of Nikon 8 x 40 binoculars for the availability of fruits, flowers and immature leaves. On occasions, it was difficult to distinguish between ripe and unripe fruits due to poor visibility and, in the case of species like *Mischodon zeylanicus*, *Diospyros oocarpa*, *Hydnocarpus venenata*, and *Lepisanthes senegalensis*, due to fruit that did not show any changes in color or texture over time. Hence, ripe fruit and unripe fruit were pooled as fruit for the purpose of estimating fruit availability. Similarly, flower buds and flowers were pooled as flowers, and leaf buds and young leaves were pooled as immature leaves. Each plant part was scored at increments of 0.5 on a scale of 0.0 to 4.0 with 4 being the score for a tree with the plant part at its greatest abundance in comparison with individuals of the same species in the phonological plots. For the study area, a food availability index (FAI) for fruit, flowers and immature leaves was computed using the average monthly phenological scores and the basal area/ha value for trees within the vegetation plots in the study area (Dasilva 1994). FAI was computed using the formula:

FAI = average availability score x basal area of species i

The trees that were monitored and utilized in the computation of FAI fruits, flowers and immature leaves within the study area included the 15 most frequently utilized tree species by the three groups (all three combined) and accounted for approximately 80% of the proportion feeding time of group A and B and 74% of the proportion of feeding of *T. vetulus*.

4.2.5 Behavioral data collection

Behavioral data were collected for at least 5-8 days a month for each of the groups. On each day, observations began at dawn when the monkeys left their sleeping trees and ended at dusk when the monkeys entered their sleeping trees. During the course of observation, the locations at which each group became stationary to feed were recorded using a Garmin 76 CSX GPS receiver. The center of the group was visually determined and recorded as the location of the group (Fashing et al. 2007). Hence, the daily path length on a given day was considered to be the linear distance between successive feeding bouts. The positional data were transferred to ArcView 9.3 (ESRI), and Hawth's Analysis Tools module (http://www.spatialecology.com/htools) was used to compute daily path lengths and home-range size. During the course of observation, due to challenges posed by the terrain of the study site, observers would often lose sight of the monkeys for short periods (15-25 minutes) during the day when following the monkeys from one location to another. The positional data from such days were not used in computing daily path lengths. Hence, the daily path lengths reported here for each group correspond to days on which the observer was in contact with the group at all times. Home range size is defined here as the area included within a minimum convex polygon (MCP) encompassing all location data points collected during the study period.

The index of defendability (*D*) (Mitani and Rodman 1979) was computed as a measure of intensity of home range use. The index compares average day length (*d*) in relation to the diameter of a circle (*d'*) with an area equal to the observed home range (A). *D* was computed for each group for months for which daily path length was estimated using the formula:

$$D = d/(4A/\pi)^{0.5}$$

A high *D* value, which implies frequent contact with home range boundaries at widely separating points on the perimeter, is indicative of intense home range use (Nunn and Dokey 2006). *D* values ≥ 1 have been typically reported for territorial species, while *D* values ≤ 1 have been largely reported from nonterritorial species (Mitani and Rodman 1979).

The relationship between daily path length and food availability was explored using Spearman rank-order correlation coefficients (r_s) between monthly average daily path length and fruit, and flower and immature leaf availability corresponding to those months (Fashing 2001). The relationship between daily path length and monthly average rainfall was also explored using Spearman rank-order correlation coefficients (r_s) between monthly average daily path length and mean monthly rainfall (Fashing 2001). Kruskal-Wallis tests were performed to compare daily path lengths between the groups.

4.3 Results

4.3.1 Forest composition and food availability

In the 59 plots that were used to characterize the vegetation at the Kaludiyapokuna forest reserve, a total of 2110 trees were encountered from 73 species, belonging to 58 genera and 30 families. The DBH of trees at Kaludiyapokuna ranged from 9.0 cm to 275.2 cm with a mean and mode of 24.4 cm (SD ± 23.61) and 9.0 cm respectively. The stem density, species composition and DBH of trees within the home ranges of the three groups were similar and hence the food availability within the home ranges of the three groups could be considered to be similar. Table 4.2 gives the tree species composition within the home ranges of the three primate groups.

The availability of fruit, flowers and immature leaves measured as FAI units/ha, varied considerably from month to month (Fig. 4.1). Fruit availability was lowest during the month of March and highest during the month of June. The availability of flowers was highest during the month of August and lowest during December and January. Immature leaf availability was at it lowest during the month of February and highest during September. Mature leaves were the most abundant food item available throughout the year.

4.3.2 Home range and daily path length

The total home ranges of the two *S. entellus* groups A and B were 9.4 ha and 7.8 ha respectively. In comparison the home range of *T. vetulus* was 11.1 ha (Fig. 4.2). When the cumulative home range of the three groups were plotted, the curve reached asymptote for Groups A and B but not for *T. vetulus*. This suggests that the home range reported here for Groups A and B are likely complete while the figure reported for *T. vetulus* is likely to be the partial home range of the group (Fig. 4.3). The overlap between Group A and *T. vetulus* was extensive (6.1 ha), while the overlap between Groups A and B was minimal (1.8 ha). The home range of *T. vetulus* also overlapped with the home ranges of at least two other *S. entellus* groups that were not a part of this study. The home range of Group B also overlapped with the home range of another *T. vetulus* group that was not part of this investigation.

The average daily path length for Group A and Group B during the study period was 441 m (SD ± 123) and 348 m (SD ± 135), respectively. In comparison the average daily path length of *T. vetulus* during the study was 251 m (SD ± 123). The variation in daily path length between the three groups was statistically significant (Kruskal-Wallis test $p \leq 0.001$). The mean defendability index (*D)* was higher for Groups A and B in comparison to *T. vetulus* (Table 4.3). This suggests that home range use by *S. entellus* was more intense in comparison to *T. vetulus*. Table 4.3 gives the monthly average daily path length and *D* for the three study groups for the duration of the study period.

4.3.3 The effect of food availability and rainfall on daily path length

In the case of Group A, monthly average daily path length was negatively correlated with fruit availability during those months but there was no statistically significant relationship between monthly average daily path length and flower and immature leaf availability (Table 4.4). In comparison, the correlations between monthly average daily path length and food item availability for Group B were statistically significant. In the case of *T. vetulus*, the correlations between monthly average daily path length and food item availability was also not statistically significant. Monthly rainfall had no statistically significant effect on monthly average daily path length of Group A (n =10; r_s= -0.103; p $\leq$ 0.777), Group B (n = 7; r_s= -0.036; p $\leq$ 0.939) and *T. vetulus* (n = 6; r_s= -0.377; p $\leq$ 0.461).

4.4 Discussion

The results of this study show that *T. vetulus* and *S. entellus* at Kaludiyapokuna differed in several aspects of their ranging behavior. Certain aspects of the ranging pattern of *T. vetulus* and *S. entellus* also differed significantly from patterns reported for these species at other study localities.

The home range size of *T. vetulus* at Kaludiyapokuna was much larger than that reported for the species at Polonnaruwa (Table 4.5). Several studies published on the ranging behavior of primates have shown food resources to be an important determinant of size, with home range size shown to decrease with the increase in food resources (Mckey and Waterman 1982; Terborgh 1983). Home range size within species has also been shown to increase with group size (Ostro et al. 1999; Teichroeb and Sicotte 2009) and decrease in relation to the density of conspecifics (Fashing 2001). Thus, it is possible that the home range size reported for *T. vetulus* at Kaludiyapokuna could be due to large group size or due to comparatively low density of conspecifics. At Polonnaruwa the average group size for *T. vetulus* was 8.4 individuals per group (Rudran 1973b) and the population density of the species is among one of the highest for colobine populations in the world (Davies 1994). Since stem density and plant species richness was comparatively higher at Kaludiyapokuna in comparison with Polonnaruwa (Dittus 1977), resource availability is unlikely to have caused the difference in the home range size between *T. vetulus* at Kaludiyapokuna and Polannaruwa.

The home range size of *S. entellus* at Kaludiyapokuna was much smaller in comparison to the home range size reported for the species from Polonnaruwa and India (Table 4.5). The discrepancy in the home ranges reported for *S. entellus* in this study and previous studies may be due to differences in the sizes of the study groups, density of conspecifics, or differences in resource availability between study localities. In general, the group sizes reported for *S. entellus* at Polonnaruwa and India are larger (Davies 1994) in comparison with the Kaludiyapokuna where *S. entellus* averaged 15 animals per group. The density of *S. entellus* at Polonnaruwa (Davies 1994) was much higher in comparison with the density of *S. entellus* at Kaludiyapokuna, which was 53 animals/km^2. At Kaludiyapokuna, Group A (n= 22) had a larger home range than Group B (n=13). Since the vegetation compositions within the home ranges of both groups were relatively similar, it is unlikely that the difference in home range size between Group A and B is due to differences in resource availability but rather reflects the higher energetic demands of Group A. Similar associations between group size and home range size have also been observed in other foli-frugivorous primates (Ostro et al. 1999; Gillespie and Chapman 2001).

The daily travel patterns of primates are influenced by a number of factors such as the availability of food resources (Newton 1992; Di Fiore 2003; Matsuda et al. 2009), group size (Gillespie and Chapman 2001), and weather (Olupot et al. 1997). The average daily path length of *T. vetulus* at Kaludiyapokuna is comparable with other *Trachypithecus* species (Table 4.5). In contrast, the average daily path length of *S. entellus* in this study is short in comparison to observations made on the species elsewhere. In spite of both Group A and B occupying ecologically similar habitats, the average daily path length of Group A was greater than the average daily path length of Group B. Although the sample size here is too small to make generalizations on the influence of group size on primate ranging patterns, the difference in the daily path lengths between Groups A and B lends support to the hypothesis that if food availability is held constant an increase in group size should lead to an increase in day-range length as within-group scramble competition increases with increase in group size (Janson and Goldsmith 1995; Teichroeb and Sicotte 2009). Thus, the longer daily path length of Group A may be a response by the group to mitigate higher levels of within-group scramble competition experienced by the group in comparison to Group B. However, more recently, alternative hypotheses such as the resource dispersion hypothesis (RDH) have been proposed to explain group living in organisms that utilize patchy resources (Johnson et al. 2002). The RDH is a hypothetical model that proposes that individuals can exploit patchy resources and satisfy their needs without imposing large costs on each other. The model predicts that the animal that first enters a patch has excess resources some or all the time and hence the patch is able to sustain additional animals.

In the case of Group A, monthly average daily path length was negatively correlated with fruit. This suggests that Group A travelled farther during months when fruit availability was low. Although not statistically significant, the monthly average daily path length for Group A was also negatively correlated with flower availability. The correlations between monthly average daily path length and food item availability for Group B were not statistically significant. The negative correlation between monthly average daily path length and fruit availability in Group A also contradicts the findings of other studies on *S. entellus* (Newton 1992; Sayers and Norconk 2008) and other Asian colobines such as *Prebytis melalophos* (Bennett 1986) and *Trachypithecus pileatus* (Stanford 1991), which showed these primates to travel farther when the diet was dominated by fruits and flowers rather than by leaves. The results of this study together with other published works on these aspects suggests that there is considerable inter- and intra-specific variation in how primates alter their ranging behavior in response to changes in resource availability and no single ecological strategy can characterize the behavior of a particular primate species.

In addition to food availability, other factors such as the amount of rainfall (McKey and Waterman 1982) and availability of sleeping trees (Matsuda et al. 2009) have also been shown to influence the ranging behavior of primates. In the case of *T. vetulus* and *S. entellus* in this study, mean monthly rainfall had no statistically significant impact on ranging behavior.

In this study, *S. entellus* and *T. vetulus* also differed significantly in their intensity of home range use. *Trachypithecus vetulus* had a low defendability index (*D*) in comparison to *S. entellus*, which indicates that *T. vetulus* travelled a relatively short distances on any given day in comparison to *S. entellus* and consequently utilized only a fraction of its total home range. This observation is consistent with the behavior of *T. vetulus* at Polonnaruwa, where the species was reported to adopt a less mobile system (Hladik 1977). This behavior is probably advantageous, given the extensive nature of home range overlap between the two species. Low mobility probably reduces direct contact between

T. vetulus and *S. entellus* and promotes temporal niche partitioning, a situation where the two species can utilize shared areas of their home ranges at different times reducing ecological competition. The pattern of home range overlap between the two *S. entellus* groups and between species in this study was similar to the observations made for these species at Polonnaruwa (Hladik 1977). However, the low defendability (*D*) observed for *T. vetulus* in this study contradicts the behavior of *T. vetulus* at Polonnaruwa, which has been reported as being extremely territorial (Rudran 1973b). Low defendability (*D*) has been typically reported for species which display low levels of territoriality (Mitani and Rodman 1979). The low defendability (*D*) for *T. vetulus* in this study is possibly the result of the relatively low density of the species at the study site (19 animals/km^2) in comparison to Polonnaruwa (100-200 animals/ km^2) (Davies 1994). The low density of conspecifics probably alleviated the need for the *T. vetulus* group to regularly traverse its entire home range to monitor and deter other conspecific groups from intruding. Conversely, the relatively high population density of *S. entellus* at the study site (53 animals/ km^2) probably required Groups A and B to regularly traverse their home ranges to deter potential intrusion from conspecific groups, which probably resulted in a comparatively higher index of defendability (*D*).

The results of this study show that *T. vetulus* and *S. entellus* differed in several aspects of their ranging behavior and also differed from the findings of previous studies investigating the ranging behavior of these species. The home range of *T. vetulus* in this study was much larger than home range for the species at Polonnaruwa (Hladik 1977). The home range of *S. entellus* in this study was much smaller than the home range previously reported for the species. The overlap between *S. entellus* and *T. vetulus* in this study was extensive and was similar to the patterns of overlap between these species at Polonnaruwa (Hladik 1977). *Trachypithecus vetulus* at Kaludiyapokuna also adopted a strategy of low mobility which probably minimizes contact with *S. entellus* and promotes the coexistence of the two species. Although the generalizability of the results of this study are limited due to the small sample of daily path lengths and study groups, the study does elucidate relationships between group size, food availability, and ranging behavior of these primates and these realtionships warrant further rigorous examination in the future.

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4.6 Tables

Table 4.1. Composition of study groups. AM= Adult male, AF= Adult female, SA= Sub adult, JV= Juvenile, IN = Infant.

Species	AM	AF	SA	JV	IN	Total
S. entellus						
Group A	3	7	3	7	2	22
Group B	2	5	1	4	1	13
T. vetulus	1	6	0	0	4	11

Table 4.2. Tree composition in the home ranges of the three groups. *= Tree species included in the ten most frequently utilized plant species by the three groups.

	Group A (*S. entellus*)		Group B (*S. entellus*)		*T. vetulus*	
Area sampled (ha)	1		0.52		0.48	
Number of species	48		37		30	
Number of families	24		19		19	
Stem density (stems/ha)	643		675		698	
DBH						
Mean (95% CI)	24.3 (22.5 26.1)		25.3 (22.6 28.0)		22.0 (20.0 24.0)	
Mode	9.0		10.5		9.0	
The 20 highest-ranking trees	Family	Species (BA/ha, relative BA/ha)	Family	Species (BA/ha, relative BA/ha)	Family	Species (BA/ha, relative BA/ha)
	Ulmaceae	*Holoptelea integrifolia* (83968, 15.1)*	Moraceae	*Ficus microcarpa* (117702, 17.4)	Euphorbiaceae	*Drypetes sepiaria* (91747, 20.5)*
	Euphorbiaceae	*Drypetes sepiaria* (76309, 13.7)*	Moraceae	*Ficus amplissima* (79088, 11.7)	Moraceae	*Ficus microcarpa* (61443, 13.8)*
	Moraceae	*Ficus microcarpa* (74749, 13.4)*	Ulmaceae	*Holoptelea integrifolia* (70734, 10.5)	Flacourtiaceae	*Hydnocarpus venenata* (51509, 11.5)
	Euphorbiaceae	*Mischodon zeylanicus* (35250, 6.3)*	Sterculiaceae	*Pterygota thwaitesii* (63050, 9.3)	Euphorbiaceae	*Mischodon zeylanicus* (49218, 11.0)*
	Flacourtiaceae	*Hydnocarpus venenata* (34182, 6.1)*	Sterculiaceae	*Pterospermum suberifolium* (39400, 5.8)*	Datiscaceae	*Tetrameles nudiflora* (23571, 5.3)*
	Sterculiaceae	*Pterospermum suberifolium* (29648,5.3)	Euphorbiaceae	*Drypetes sepiaria* (39226, 5.8)*	Ebenaceae	*Diospyros oocarpa* (22982, 5.1)*
	Annonaceae	*Diospyros oocarpa* (24023, 4.3)	Ebenaceae	*Diospyros oocarpa* (37129, 5.5)	Sterculiaceae	*Pterospermum suberifolium* (20978, 4.7)
	Datiscaceae	*Terameles nudiflora* (22628 4.0)*	Euphorbiaceae	*Mischodon zeylanicus* (27530, 4.1)*	Sapindaceae	*Lepisanthes senegalensis* (14940, 3.3)
	Ebenaceae	*Diospyros ebenum* (14908, 2.7)	Lauraceae	*Cryptocarya sp.* (23035, 3.4)	Fabaceae	*Dialium ovoideum* (13801, 3.1)*
	Annonaceae	*Xylopia nigricans* (13477, 2.4)	Sapindaceae	*Dimocarpus longan* (19981, 2.9)	Annonaceae	*Xylopia nigricans* (13718, 3.1)
	Lauraceae	*Cryptocarya* sp. (12019, 2.2)	Verbenaceae	*Vitex altissima* (16792, 2.5)*	Ebenaceae	*Diospyros oocarpa* (13101, 2.9)
	Sapotaceae	*Manilkara hexandra* (11615, 2.1)*	Annonaceae	*Xylopia nigicans* (15242, 2.2)	Tiliaceae	*Grewia rothii* (10248, 2.3)
	Aponogetonaceae	*Wrightia angustifolia* (10333, 1.8)*	Euphorbiaceae	*Dimorphocalyx glabellus* (12244, 1.8)	Anacardiaceae	*Spondius dulcis* (8090, 1.8)
	Sapindaceae	*Lepisanthes senegalensis* (9518, 1.7)	Fabaceae	*Dialium ovoideum* (12064, 1.8)*	Ebenaceae	*Diospyros ovalifolia* (7820, 1.8)
	Fabaceae	*Dialium ovoideum* (9448, 1.7)	Ebenaceae	*Diospyros ebenum* (11710, 1.7)	Lauraceae	*Cryptocarya* sp. (5519, 1.2)
	Tiliaceae	*Grewia rothii* (8739, 1.6)*	Tiliaceae	*Grewia rothii* (9438, 1.4)*	Ulmaceae	*Holoptelea integrifolia* (5115, 1.1)
	Sterculiaceae	*Pterygota thwaitesii* (8128, 1.4)	Clusiaceae	*Mesua ferrea* (9294, 1.4)	Sapindaceae	*Dimocarpus longan* (4801, 1.1)
	Euphorbiaceae	*Dimorphocalyx glabellus* (7117, 1.3)	Datiscaceae	*Tetrameles nudiflora* (7073, 1.0)*	Sapindaceae	*Lepisanthes tetraphyla* (4644, 1.0)
	Sapindaceae	*Dimocarpus longan* (6718, 1.2)	Aponogetonaceae	*Wrightia flavido-rosea* (7007, 1.0)	Aponogetonaceae	*Wrightia angustifolia* (4519, 1.0)*
	Verbenaceae	*Vitex altissima* (6708, 1.2)*	Annonaceae	*Polyalthia coffeoides* (6989, 1.0)	Aponogetonaceae	*Wrightia tomentosa* (3169, 0.7)

Table 4.3. Monthly mean daily path length and the number of complete daily path lengths collected for the study groups during the study period. MMDPL= Monthly mean daily path length; *D* = Index of defendability.

Month	Group A			Group B			*T. vetulus*		
	No. of paths	MMDPL (m)	*D*	No. of paths	MMDPL (m)	*D*	No. of paths	MMDPL (m)	*D*
July 2008	3	400	1.2	3	497	1.6	-	-	-
August 2008	5	353	1.0	2	478	1.5	-	-	-
September 2008	2	435	1.3	-	-	-	-	-	-
October 2008	2	358	1.0	-	-	-	-	-	-
November 2008	-	-	-	-	-	-	-	-	-
December 2008	4	454	1.3	4	326	1.0	-	-	-
January 2009	5	472	1.4	6	320	1.0	3	277	0.7
February 2009	4	559	1.6	4	276	0.9	6	241	0.6
March 2009	4	411	1.2	-	-	-	3	310	0.8
April 2009	2	508	1.5	4	325	1.0	4	232	0.6
May 2009	1	477	1.4	2	306	1.0	2	210	0.6
June 2009	-	-	-	-	-	-	3	238	0.6
Mean (±SD)	-	441 (±123)	1.3 (1.9)	-	348 (± 135)	1.1 (0.3)	-	251 (± 123)	0.6 (0.1)

Table 4.4. Spearman rank-order correlation coefficients (r_s) for monthly average daily path length versus plant part availability. MADPL=Monthly average daily path length. *= $p \leq 0.05$

Study group	MADPL vs FAI fruit (*n*, p ≤)	MADPL vs FAI flowers (*n*, p ≤)	MADPL vs FAI immature (*n*, p ≤)
Group A	-0.673 (10, 0.033)*	-0.576 (10, 0.082)	-0.309 (10, 0.385)
Group B	0.643 (7, 0.119)	0.429 (7, 0.337)	0.571 (7, 0.180)
T. vetulus	-0.489 (6, 0.329)	0.257 (6, 0.623)	-0.600 (6, 0.208)

Table 4.5. A comparison of ranging data from 11 Asian colobine species. *= home range computed using a 0.4 x 0.4 ha grid; # = home range computed using a 500 m X 500 m grid.

Species	Mean DPL (m)	DPL (Range)(m)	Home range (ha)	Study site	Reference
Presbytis melalophus	703	300-1360	30	Kuala Lompat, Malaysia	Bennett (1986)
Presbytis potenziani	540	60-1120	33	Betumonga, Indonesia	Fuentes (1996)
Presbytis rubricunda	850	225-1670	85	Sepilok, Malaysia	Bennett and Davies (1994)
Presbytis rubricunda	-	-	35-99	Tanjung Puting, Indonesia	Supriatna et al. (1986)
Trachypithecus johnii	-	-	24	Kakachi, India	Oates et al. (1980)
Trachypithecus pileatus	325	50-700	22	Madhupur, Bangladesh	Stanford (1991)
Trachypithecus leucocephalus	491	-	23.8	Fusui Nature Reserve, China	Zhou et al. (2011)
Trachypithecus leucocephalus	512	-	33.8	Fusui Nature Reserve, China	Zhou et al. (2011)
Trachypithecus francoisi	438	-	19	Fusui Nature Reserve, China	Zhou et al. (2007)
Trachypithecus vetulus	-	-	2-3	Polonnaruwa. Sri Lanka	Hladik (1977)
Trachypithecus vetulus	251	131-409	11	Kaludiyapokuna, Sri Lanka	This study
Semnopithecus entellus	1083	-	75	Kanha, India	Newton (1992)
Semnopithecus entellus	2990	-	1250*	Junbesi, Nepal	Curtin (1982)
Semnopithecus entellus	-	-	10-15	Polonnaruwa. Sri Lanka	Hladik (1977)
Semnopithecus entellus	441	189-650	9.4	Kaludiyapokuna, Sri Lanka	This study
Semnopithecus entellus	348	111-632	7.8	Kaludiyapokuna, Sri Lanka	This study
Nasalis larvatus	910	370-1810	221	Sukau, Malaysia	Boonratana (2000)
Nasalis larvatus	799	220-1734	138	Kinabatangan, Sabah, Malaysia	Matsuda et al. (2009)
Rhinopithecus bieti	1310	300-2950	$1625^{\#}$	Wuyapiya, China	Kirkpatrick et al. (1998)

4.7 Figures

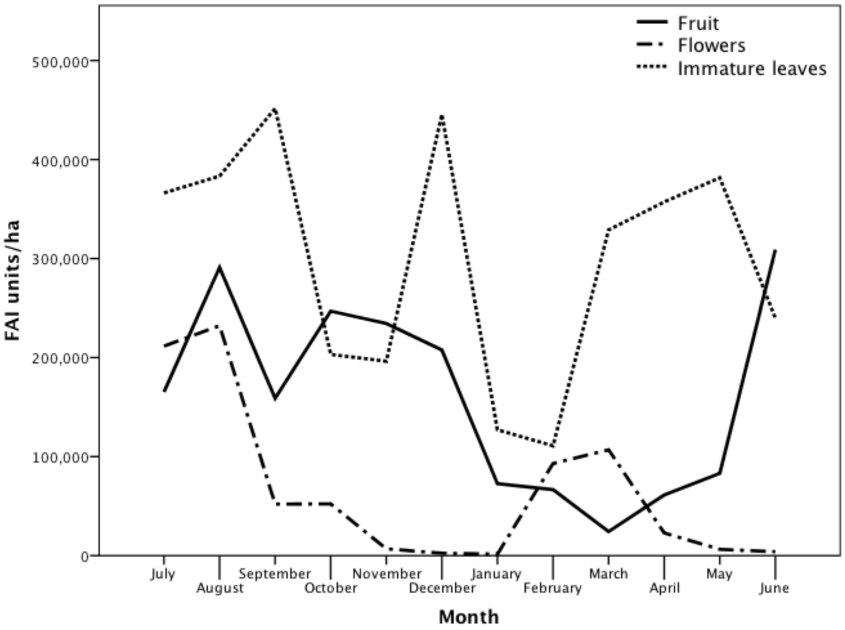

Figure 4.1. Monthly variation in fruit, flower and immature leaf availability in FAI units/ha in the study site from July 2008 to June 2009.

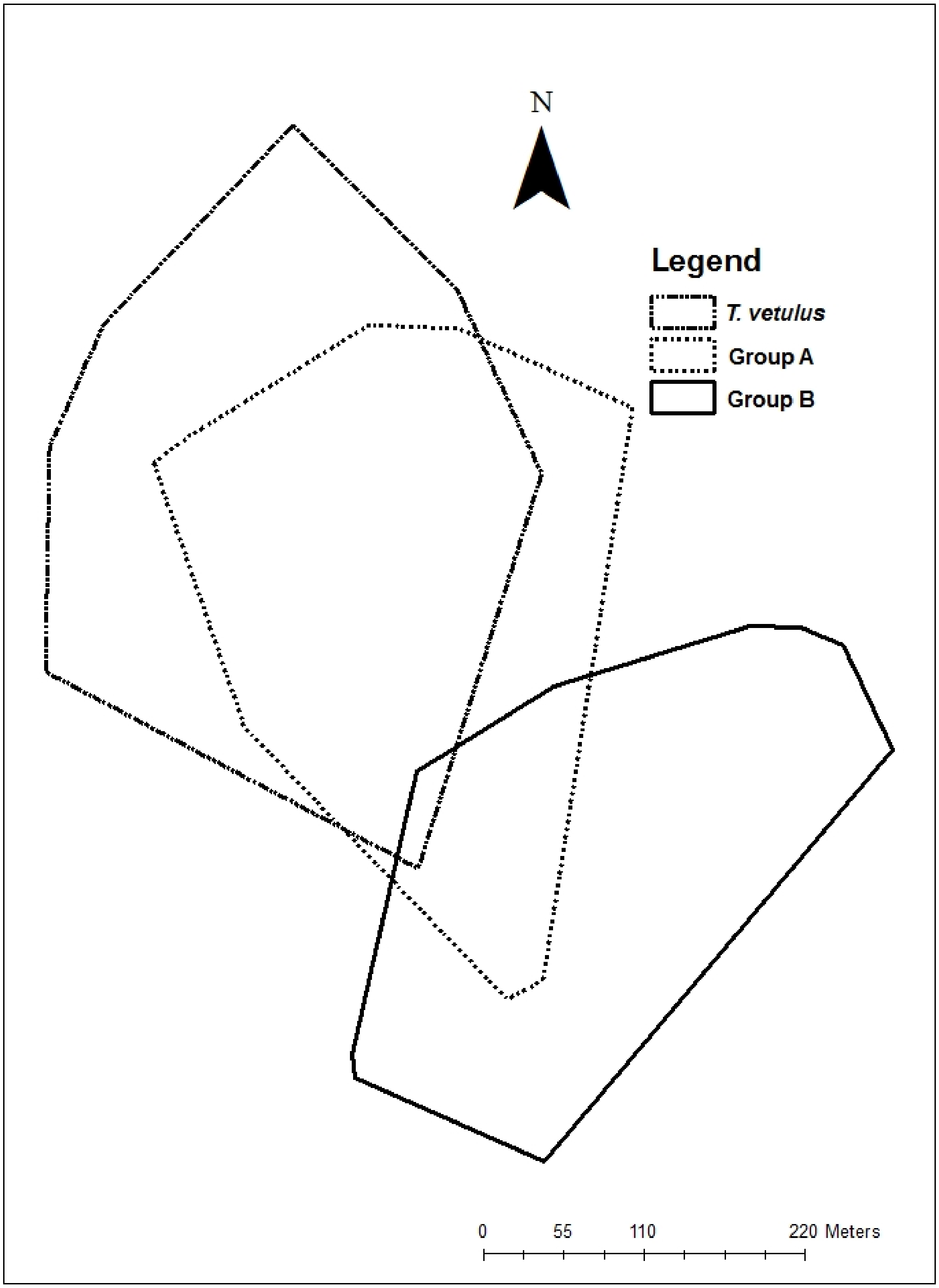

Figure 4.2. Home ranges of *T. vetulus* and *S. entellus* Groups A and B.

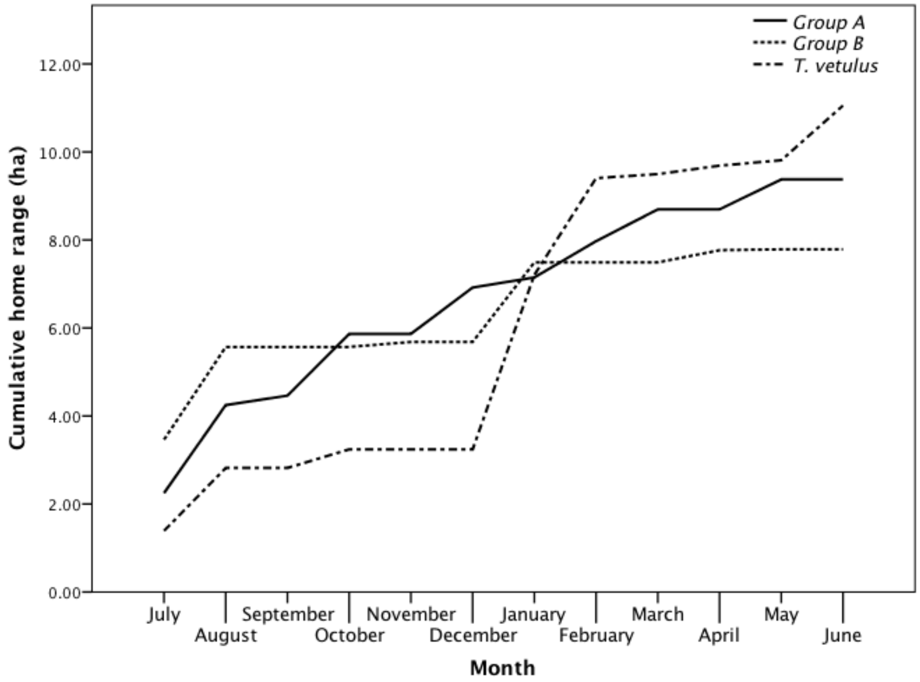

Figure 4.3. Cumulative monthly home range of *T. vetulus* and Groups A and B.

Chapter 5

Dietary overlap, habitat use and interspecific interaction in *Trachypithecus vetulus* and *Semnopithecus entellus* in the Kaludiyapokuna forest reserve in the dry zone of Sri Lanka.

5.1. Introduction

Understanding how niche differences evolve in species on the same trophic level and how these differences are maintained ecologically is a fundamental question in ecology (Hubbell 2005). Numerous authors have acknowledged the existence of regular patterns within communities such as distribution complementarities (Toft et al. 1982; Gilpin and Diamond 1982), resource partitioning and the temporal variation in the degree of resource partitioning (Schoener 1986; Korpimaki 1987), character displacement (Brown and Wilson 1956), habitat shifts (Schoener 1975; Diamond 1978) and niche expansion (Lister 1976). A number of biotic interactions such as mutualism (van der Heijden et al. 1998; Stachowicz 2001), predation (Turner and Mittleback 1990) and competition (Pacala and Roughgarden 1985) as well as abiotic interactions like climatic effects (Weins 1977) have been shown to create niche partitioning and other patterns in ecological communities. Competition has been shown to alter population densities (Hairston 1951), foraging efficiency, growth rate (Dunham 1980; Gustafsson 1987; Ziv and Kotler 2003), age structure (Smith 1981), habitat use (Creel and Creel 1996), and activity patterns (Kotler et al. 1993; Jones et al. 2001). Competition is widely regarded as one of the more important ecological interactions and holds a central place in evolutionary theory (MacArthur and Levins 1964, 1967; Gurevitch et al. 1992). However, its relative importance has been debated in recent years (Stachowicz 2001; Hubbell 2005).

Two approaches have been used to assess the role of interspecific competition in shaping the niches of coexisting species. The first approach compares niche of organisms in the presence of competitors with niches of the organisms in the absence of competitors (Huey et al. 1974; Schoener 1975; Diamond 1978; Alatalo et al. 1985; Ziv and Kotler 2003). These studies show that species alter aspects of resource utilization such as feeding rates (Ziv and Kotler 2003) and habitat use (Alatalo et al. 1985) when in the presence of potential competitors to reduce resource overlap with competitors. The second approach compares resource use in coexisting putative competitors in relation to resource availability (Lack 1947; Smith et al. 1978; Lister 1980; Toft 1980; Korpimaki 1987; Holbrook and Schmitt 1989; Nakano et al. 1999). These studies show that coexisting putative competitors display greater niche partitioning during periods of resource scarcity in comparison with periods of resource abundance.

Competition also holds a central place in primate socioecology. Identifying the different factors that influence primate group size and social organization has been an important theme (Chapman et al. 1995; Steenbeek and van Schaik 2001). However, the broader role of interspecific competition in primate communities is unclear as relatively few studies have addressed this topic precisely (Gautier-Hion 1980; Guillotin et al. 1994; Tutin et al. 1997; Stevenson et al. 2000; Agostini et al. 2010; Houle et al. 2010; Singh et al. 2011). The majority of these studies have examined only a few lines of evidence, mainly change in diet overlap in relation to resource availability (Tutin et al. 1997; Guillotin et al. 1994; Gautier-Hion 1980) and only a few have attempted to collect quantitative data on species interaction (Stevenson et al. 2000; Houle et al. 2010; Singh et al. 2011). The studies that examine the variation in dietary overlap assume that the observed pattern of dietary overlap is the outcome of interspecific competition. However, similar patterns can also arise as a result of species making shifts in diet as a result of dietary flexibility facilitated by physiological and morphological adaptations (Korpimaki 1987). Hence, the results of these studies are inconclusive. Despite the paucity of studies that examine the interactions of primate species in a community, several lines of evidence indicate that interspecific competition is an important ecological interaction in determining primate community structure. These include: density compensation by medium-sized non-hunted primates such as *Pithecia* and *Cacajao* after the extinction of large-bodied primates such as *Alouatta*, *Lagothrix* and *Ateles* (Peres and Dolman 2000); positive correlation between ratios of body mass and the number of species at a site (Ganzhorn 1999); body size mediated dominance hierarchies in tropical frugivores (French and Smith 2005); and aggressive interactions between species (Stevenson et al. 2000). However, this evidence for interspecific competition is largely from frugivorous primate communities and hence the influence of interspecific competition on the ecology of foli-frugivorous species such as colobine monkeys is poorly understood.

Due to their unique dietary specializations colobines are capable of ingesting large quantities of foliage and hence the group as a whole is often labeled as ‘the leaf eaters’. Hairston et al. (1960) suggested that herbivores do not compete for food partly because resources are not limited. Leaves have been identified as key food resource for colobines and since leaves are superabundant and evenly dispersed, it is often assumed that within-group exploitation competition is weak or absent (Ripley 1970; McKenna 1979; Wrangham 1980; Steenbeek and van Shaik 2001). Contrary to these predictions, several lines of evidence suggest that folivorous primates are food limited. A number of studies have shown that colobines are not mere obligate folivores and preferentially select high quality foods such as young leaves, fruit and seeds which are distributed in patches that are irregularly distributed in space and time (Oates 1994; Davies et al. 1999; Chapman et al. 2002a). Also the availability of food, especially high quality foods, has been shown to account for much of the variation in colobine biomass (McKey et al. 1981; Waterman et al. 1988; Chapman et al. 2002a). In addition, contest competition has also been documented in colobine monkeys (Koenig 2000; Koenig et al. 2004). Finally, Gillespie and Chapman (2001) in their test of the ecological constraints model on red colobus found that a larger group had longer day ranges than a smaller group and that the day range of the larger group increased further in response to decreased food availability. These observations indicate that aspects of the ecology of colobine monkeys are influenced by the availability of food, and thus it is probable that competitive interactions occur between colobine species within a community.

Trachypithecus vetulus and *Semnopithecus entellus* are two species of colobine monkeys that inhabit the island on Sri Lanka. *Trachypithecus vetulus,* which is predominantly confined to the wetter regions of Sri Lanka, overlaps with *Semnopithecus entellus*, which is confined to the drier lowlands, in the north central dry zone of Sri Lanka (Bennett and Oates 1994). However, it is relatively rare to find forests that support healthy populations of both species. Much of what is known about the ecology of *S. entellus* (Ripley 1965; 1967; 1970) and *T. vetulus philbricki* (Hladik 1977) in Sri Lanka is from studies carried out at Polonnaruwa sanctuary, a secondary semi-evergreen dry zone forest in the north central region and more recently from a study on *T. vetulus nestor* in home gardens and rubber plantations in the Western Province of Sri Lanka (Dela 2007). Only the study by Rudran (1973a; 1973b) on the group structure and reproduction of *T. vetulus monticola* was carried out in an undisturbed habitat in Sri Lanka. Ripley (1965; 1967; 1970) studied the social organization and behavior of *S. entellus* at Polonnaruwa. Hladik (1977) compared the feeding behavior of sympatric *S. entellus* and *T. vetulus* at Polonnaruwa and found that *S. entellus* was less arboreal and more frugivorous and utilized a more diverse array of plants than *T. vetulus*. *Trachypithecus vetulus* was observed to display a low level of mobility and maintained small home ranges averaging 2.5 ha in comparison to *S. entellus*, which ranged over a wide area and maintained home ranges of 10 to 15 ha. Although the two species were shown to ingest different proportions of fruit, flowers and immature leaves, in these studies the investigators did not investigate interspecific interaction and variation in ecological overlap between the two species in relation to the availability of patchy resources such as fruit and flowers and hence failed to examine the role of interspecific overlap on the primate community. Since Hanuman langurs inhabit the extremely wet regions of India (Jay 1965), Ripley (1965) hypothesized that the presence of *T. vetulus* in the wet zone of Sri Lanka has prevented the hanuman langur from colonizing the wet zone forests of Sri Lanka. At Polonnaruwa, hanuman langurs and purple-faced langurs were observed to avoid each other in areas where their home ranges overlap (Ripley 1965). Thus it is possible that interspecific competition is an important interaction influencing the ecology of these species and thereby the geographic distribution of these primate species.

In this chapter, I analyze diet overlap of seasonal resources such as fruit and flowers between *T. vetulus* and *S. entellus* and interspecific interaction to assess the role of interspecific competition in shaping aspects of the niches of these coexisting primate species. I specifically analyze how fruit and flower overlap varies in relation to their availability. Although overlap may not be indicative of the intensity of competition (Colwell and Futuyma 1971; Abrams 1980), changes in overlap or the degree of resource partitioning may better reflect the influence of interspecific competition (Korpimaki 1987). As observed in many ecologically similar species such as predatory birds (Korpimaki 1987), primates (Guillotin et al. 1994; Tutin et al. 1997) and fish (Nakano et al. 1999), niche overlap between the primates in this study (degree of resource partitioning) should be greatest during periods when resources like fruit, flowers and shoots are abundant, with reduced overlap during periods when they are scarce. Since field experiments have shown species to alter their rate of resource use when in the presence of competitors (Ziv and Kotler 2003), this study also compares feeding effort when the two species were in close proximity to each other and when they are not. I predicted that if competition occurred and one species displaced the other from feeding sites, then the feeding effort of one or both species should be lower when in association than when they are not. In addition, I also examined if either species excludes the other by comparing the vertical dispersion of the two species while foraging, when they are in association and when they were not.

In addition to addressing the importance of interspecific competition on primate communities, the results of this study highlight resource use patterns in these primates that enable them to coexist when sympatric and contribute towards broadening our understanding of the ecology of these species.

5.2 Material and methods

5.2.1 Study site

The study was conducted in the Kaludiyapokuna forest reserve (N 07° 52.5, E 080° 44.1) located in the Matale district in the north central dry zone of Sri Lanka. The study was conducted under the authority of the Department of Wildlife Conservation of Sri Lanka and in collaboration with the University of Peradeniya, Sri Lanka. The main study area is approximately 2.2 km^2 in extent and is contiguous with the Knuckles forest range in the south. The study site is surrounded by farmland and human settlements from the north, east and west. The study site is undisturbed by humans and the primates are not provisioned, unlike the Polonnaruwa study site, which is disturbed and where primates have become accustomed to humans through regular contact (Bishop et al. 1981). Also there is no evidence to indicate that hunting, timber extraction or woodcutting has occurred at the site. The study site supports populations of four species of primates as well as populations of other herbivorous mammals such as Asian elephants (*Elephas maximus*), spotted deer (*Axis axis*), sambar deer (*Cervus unicolor*), and wild pig (*Sus scrofa*). Unlike Polonnaruwa (Bishop et al. 1981), this study area is home to a full complement of potential primate predators such as the black eagle (*Ictinaetus malayensis*), leopard (*Panthera pardus*) and python (*Python molurus*).

The study area receives about 1250 mm of rainfall annually (Fig. 5.1) and average temperature in the region ranges between 27-29 ^{o} C. The region receives most of its rainfall through convectional rains from October to November, which gradually grade into the northeast (NE) monsoon. The NE monsoon lasts from December to February and is most active during the month of December. The NE monsoon brings considerably less moisture than the southwestern (SW) monsoon, which lasts May to September. The northern dry zone is shielded from the SW monsoon rains by the central hills of the island and hence it experiences a characteristic period of drought during this time.

5.2.1 Subjects

In Sri Lanka, *S. entellus* is represented by a physically smaller subspecies *S. entellus thersites* (Bennette and Davies 1994) and is found throughout the well-wooded areas of the whole dry zone from south of Jaffna, in the North, to the shores of the extreme southern coast (Phillips 1935). The purple-faced leaf monkey, *T. vetulus* is endemic to Sri Lanka and is divided into four distinct subspecies all occupying different geographic regions. *T. vetulus philbricki,* the northern dry zone subspecies, shares its range with *S. entellus.*

Dietary data were collected over a 12-month period between July 2008 and June 2009 as part of a long-term study of the comparative ecology of *T. vetulus* and *S. entellus* in Sri Lanka. Data collection was confined to one *S. entellus* and one *T. vetulus* group. The groups had overlapping home ranges and, at the time of data collection, were habituated to human observers and could be approached to within a distance of 10 m without showing signs of alarm or panic. The composition of the study groups is given in Table 5.1.

5.2.2 Forest composition

Vegetation sampling was carried out using vegetation plots (Ganzhorn 1989). Localities for sampling were chosen with the aid of a WorldView 1 satellite image of the study area and care was taken to ensure that the localities were evenly distributed across the study area so that an unbiased representative sample of the vegetation could be obtained. Each plot was 20 x 20 m in extent and 59 plots were used to sample the vegetation at the study site. Trees that were greater than 9 cm in diameter at breast height (DBH) and woody lianas were measured using a DBH tape. Plant samples were collected and herbarium sheets were prepared. The specimens were identified and compared to voucher specimens at the National Herbarium at the Royal Botanical Gardens, Peradeniya, Sri Lanka. The basal area (BA) for each tree was calculated using the formula:

$$BA = [0.5 \times DBH]^2 \times \pi.$$

The measure BA per hectare was used to define the biomass of each plant species within the home range of each group (Fashing 2001).

To describe the vertical and horizontal structure of the forest the line intercept technique as delineated by Ganzhorn (2003) was used. A 400 m baseline was setup and the height of the vegetation that came in contact with the line at 5 m intervals was recorded. The height of trees was visually estimated. Four distinct vertical strata were identified. An emergent and canopy layer composed of trees that were approximately 20-40 m in height (L1), a sub-canopy later composed of trees that were approximately 10-15 m in height (L2), an understory layer composed of saplings of tree species and shrub species that were approximately 1-5 m in height (L3) and terra firma (L4).

5.2.3 Forest phenology

To produce a quantitative measure of food availability, 958 trees and lianas in 22 phenological plots were monitored each month for phenological activity. The plant species monitored included species that were known to be consumed by the primates as well as species that were not known food species. Phenological assessment of trees was carried out with the help of two field assistants during the first week of each month. The crown of each tree was scanned by the investigator and the two field assistants for the availability of fruits, flowers, and immature leaves using Nikon 8 x 40 binoculars. On occasions, it was difficult to distinguish between ripe and unripe fruit due to poor visibility, and in the case of species like *Mischodon zeylanicus*, *Diospyros oocarpa*, *Hydnocarpus venenata*, and *Lepisanthes senegalensis*, due to fruit that did not show any changes in coloration or texture over time. Hence, ripe fruit and unripe fruit were pooled as fruit for the purpose of estimating fruit availability. Similarly, flower buds and flowers were pooled as flowers and leaf buds and young leaves were pooled as immature leaves. Each plant part was scored at increments of 0.5 on a scale of 0.0 to 4.0 with 4 being the score for a tree with the plant part at its greatest abundance in comparison with individuals of the same species in the phonological plots. A food availability index (FAI) for fruit, flowers and immature leaves was computed for the study area using the average monthly phonological scores and the basal area/ha value for trees within the vegetation plots in the study area (Dasilva 1994). FAI was computed using the formula:

FAI = average availability score x basal area of species i

The species used in the computation of FAI fruit, flowers and immature leaves within the study area accounted for the 15 most frequently utilized tree species by these primates and accounted for approximately 80% of the feeding time of *S. entellus* and 74% of the feeding time of *T. vetulus*.

5.2.4 Behavioral data collection

For at least 5-8 days a month for each of the groups, behavioral data were collected using a scan sampling technique (Altmann 1974). Group scans were conducted every 10 minutes. Efforts were made to survey all adult monkeys in each group. During each scan, the number of animals engaged in feeding, moving, resting, and in social behaviors were recorded. When an animal was spotted, the first activity that lasted longer than 3 seconds was recorded. This minimized the over-representation of eye catching ephemeral activities in the data (Fashing 2001). Feeding was considered to be any instance that involved a monkey attempting to ingest, masticate or swallow a food item. When a monkey was observed to feed during a scan, the plant species and the food item on which the animal was feeding was recorded. Food items were designated as fruit, seeds, flowers, immature leaves, and mature leaves and other items, which included sap and soil. Features such as pelage color, tail length in relation to body length, and anatomical deformities such as scars were used to identify individuals and minimize duplicating observation of individuals during behavioral data collection. During each scan, the vertical height location of each animal was also visually estimated and recorded.

When behavior data were being collected on one species, whether the other species was present in close proximity was also recorded. It was deemed that the two species were in close proximity when the distance between two individuals of the two species was less than 50 m. This cutoff was chosen because it was the furthest distance at which an observer on the ground could differentiate between groups of the two species.

An interspecific encounter rate was determined for each month by standardizing the number of encounters observed during any given month by the number of sampling days employed during that month.

Feeding effort was defined as the percentage of individuals engaged in feeding per scan (Eckardt and Zuberbuhler 2004). Monthly dietary niche overlap for fruit, flowers and immature leaves was calculated using the simplified Morisita index, (C_H) (Krebs 1989) using the formula:

$$C_H = \frac{2\sum_i^n p_{ij} p_{ik}}{\sum_i^n p_{ij}{}^2 + \sum_i^n p_{ik}{}^2}$$

The simplified Morisita's index (C_H) is an index of niche overlap between species *j* and *k*. p_{ij} is the proportion of resource *i* is of the total resource pool of species *j*, and p_{ik} is the proportion of resource *i* is of the total resource pool utilized by species *k*. This index varies between 0 and 1, with values greater than 0 indicating interspecific overlap.

Temporal patterns of dietary overlap in relation to food availability and the relationship between food availability and interspecific encounters was investigated by calculating Spearman rank-order correlation coefficients (r_s) were used to investigate the relationships between fruit, flower and immature leaf dietary overlap and availability of each plant item in the study (Fashing 2001). Spearman rank-order correlation coefficients (r_s) were also used to investigate the relationship between interspecific encounter rates and the availability of different dietary items (Fashing 2001). The Wilcoxon test was performed to evaluate if there were statistically significant differences in the feeding efforts when the two species were in close proximity and when they were not. The χ^2 test was performed to examine differences in vertical habitat use between the two species when each species was in close proximity to each other and when they were not. To control for the possible influence of variables such as season and climatic conditions on foraging effort and habitat use, for both species, scans corresponding to when one species was in close proximity to the other on a particular day were compared with scans corresponding to when the species was alone on the same day. As outlined in Chapter 1.4, it must be noted that for some of the analyses many observations of the same few numbers of individuals were included in the statistical analyses of groups. This problem cannot be eliminated in studies of free-ranging habituated groups, but the sampling protocols in effect during scans, and choice of days sampled per month, should help to minimize this problem.

5.3 Results

5.3.1 Forest composition

In the 59 plots that were used to characterize the vegetation at the Kaludiyapokuna forest reserve, a total of 2110 trees were encountered from 73 species, belonging to 58 genera and 30 families. The DBH of trees at Kaludiyapokuna ranged from 9.0 cm to 275.2 cm with a mean and mode of 24.4 cm (SD ± 23.61) and 9.0 cm respectively. Small stems (9-29 cm DBH) contributed approximately 80% of total species richness.

The number of species, families, and other statistics describing the structure of the vegetation within the home ranges of the two groups is listed in Table 5.2. The stem densities within the home ranges of the two groups were comparable. There was no statistically significant difference in the mean DBH of trees in the home ranges of the two groups (Table 5.2). There was significant overlap between the two groups in the species that ranked among the top 20 tree species in relation to basal area in their home ranges. Eighty percent of the species in the top 20 tree species in the home range of *S. entellus* was found in the home range of *T. vetulus*. In the case of both groups, Euphorbiaceae was the dominant family accounting for approximately 24% and 33% of the 20 most dominant species in the home range of *S. entellus* and *T. vetulus* respectively.

5.3.2 Forest phenology

The availability of fruit, flowers, and immature leaves measured as FAI units/ha varied considerably from month to month (Fig. 5.2). Fruit availability was lowest during the month of March and highest during the month of June. The availability of flowers was highest during the month of August and lowest during December and January. Immature leaf availability was at its lowest during the month of February and highest during September. Mature leaves were the most abundant food item and were available throughout the year.

5.3.3 Dietary overlap

The average proportion of time devoted to feeding on different dietary items during each month of the study period by *S. entellus* and *T. vetulus* is given Figure 5.3. *Semnopithecus entellus* fed on 58 positively identified species of which, 29 were exclusively used. In comparison, *T. vetulus* fed on 31 positively identified species of which only 2 were exclusively use. The species shared by *T. vetulus* and *S. entellus* each month of the study period and the time devoted to feeding on these species is given in

Table 5.3. The proportion of time devoted to feeding on shared species each month ranged from 12% to 86% for *S. entellus* and 62% to 95% for *T. vetulus*. The mean dietary overlap between *S. entellus* and *T. vetulus* was 0.34 for fruit (range 0.00-0.98), 0.23 for flowers (range 0.00-0.92) and 0.50 for immature leaves (range 0.15-0.89) (Fig. 5.4). The monthly differences between fruit, flower and immature leaf overlap between *S. entellus* and *T. vetulus* were statistically insignificant (Friedman's two-way analysis of variance by ranks $p \leq 0.174$).

In the case of *S. entellus* and *T. vetulus,* there was no statistically significant correlation between fruit overlap and fruit availability and immature leaf overlap and immature leaf availability (Table 5.4; Fig. 5.6). However, flower overlap between *S. entellus* and *T. vetulus* was positively correlated with flower availability.

5.3.4 Interspecific encounters

The rate of incidents (encounter rate) where *T. vetulus* and *S. entellus* were in close proximity ranged from 0 to 1.00 encounter per day. With the exception of two encounters during which the males of the advancing group of *S. entellus* actively displaced *T. vetulus* by whooping and chasing, all other encounters were passive in nature and involved *T. vetulus* moving into higher strata of the forest and then away from *S. entellus* as *S. entellus* entered trees occupied by *T. vetulus*. All encounters reported here occurred in the context of feeding. Most encounters between the two species occurred between January and March during the study period (Fig. 5.5).

There was no statistically significant relationship between flower and immature leaf availability and the frequency of encounters between the two species (Table 5.5).

However, there was a statistically significant negative correlation between fruit availability and the frequency of encounters between *T. vetulus* and *S. entellus*.

In the case of *S. entellus*, the percentage of animals engaged in feeding in the absence and in the presence of *T. vetulus* ranged from 20-80% and 8-90% respectively. The differences in the number of animals engaged in feeding in the presence and absence of *T. vetulus* for *S. entellus* were not statistically significant (Wilcoxon Sign Ranked Test, n = 9 $p \leq 0.260$). In comparison, for *T. vetulus*, the percentage of animals engaged in feeding in the presence and absence of *S. entellus* ranged from 8-20% and 0-15% respectively. The differences in the time devoted to feeding in the presence and absence of *S. entellus* by *T. vetulus* were statistically significant (Wilcoxon Sign Ranked Test, n = 9 $p \leq 0.008$).

5.3.5 Vertical habitat structure and interspecific influence on vertical habitat use

Chi-square analysis of habitat use by *S. entellus* and *T. vetulus*, when each species was not in close proximity (< 50 m) to the other showed that *S. entellus* occupied strata L1 and L2 less often and L3 and L4 more often than expected by chance (Table 5.6). In comparison *T. vetulus* occupied strata L1 and L2 more often and L3 and L4 less often than expected by chance. These differences were statistically significant (χ^2(3, N= 1814) = 93.54, $p \leq 0.001$).

When the two species were in close proximity, *S. entellus* continued to occupy L1 less frequently and L3 and L4 more frequently than expected by chance but also occupied stratum L2 more frequently than expected by chance (Table 5.7). Although *T. vetulus* used strata L2 more frequently than expected when *S. entellus* was not present in the vicinity, when in close proximity to *S. entellus*, *T. vetulus* occupied L2 less frequently than expected by chance. When in close proximity to *S. entellus*, *T. vetulus* occupied stratum L1 more frequently and strata L3 and L4 less frequently than expected by chance (χ^2(3, N= 666) = 32.98, p ≤ 0.001).

5.4 Discussion

The dietary overlap between *S. entellus* and *T. vetulus* at Kaludiyapokuna showed considerable temporal variation in comparison with dietary overlap between other closely related primate species (Table 5.8). However, any detailed comparison of dietary overlap indices between the species in this study to indices reported for other primate species pairs is problematic due to the variation in the methodologies adopted to compute diet overlap. Although the monthly differences between fruit, flower and immature leaf overlap as not statistically insignificant, on average immature leaf overlap was the highest, followed by fruit and flower overlap. Coincidently, of the three dietary categories considered here, immature leaves were the most abundant food item in the study area followed by fruits and flowers.

In this study, the monthly variation in fruit overlap in relation to fruit availability was not consistent with the prediction based on competition theory and observations from other primate communities which show ecologically similar sympatric species to segregate in their diet during periods of low resource production (Guillotin et al. 1994; Peres 1994; Tutin et al. 1997; Stevenson et al. 2000). In this study, fruit overlap was often high during periods of fruit scarcity as a result of both primate species utilizing the same fruit tree species. This observation is similar to the pattern of dietary overlap observed between *Saguinus fuscicollis avilapiresi* and *S. mystax pileatus*, where both species converged onto the few sources of exudates and nectar available during the dry season, resulting in high dietary overlap during that time (Peres 1996). However, it should be noted that as with *T. vetulus* and *S. entellus* at Polonnaruwa (Ripley 1965), these species at Kaludiyapokuna were never observed to occupy feeding trees at the same time. Although high fruit overlap between the primates in this study occurred during periods of fruit scarcity, it is unclear whether the level of overlap was large enough to cause competition between these two species. There is also considerable debate on the relationship between the intensity of interspecific competition and dietary overlap, as competition only becomes significant when resources are in short supply (Colwell and Futuyma 1971; Abrams 1980).

As in the case of fruit overlap, there was no statistical significant relationship between the monthly fluctuation of immature leaf overlap between the two species and monthly immature leaf availability at the study site. This is probably because immature leaves were the most abundant of the seasonal resources and were available throughout the year and hence the two species are unlikely to compete for immature leaves. However, the monthly variation of flower overlap between the two species was significantly positively correlated with monthly flower availability and hence the monthly variation in flower overlap is consistent with the predictions of competition theory and observations from a number of animal communities, which show ecologically similar species to diverge in their resource use patterns during times of resource scarcity (Lister 1980; Toft 1980; Korpimaki 1987; Holbrook and Schmitt 1989; Nakano et al. 1999). It has also been argued that morphological and behavioral adaptations may enable species to make dietary shifts similar to those caused by interference by one species on the other and exploit alternative types of food resources as preferred food items become scarce (Korpimaki 1987; Marshall and Wrangham 2007).

Interspecific interactions are known to occur between many sympatric organisms including primates (Nakano et al. 1999; Stevenson et al. 2000; Eckardt and Zuberbuhler 2004; Sushma and Singh 2006; Houle et al. 2010). In this study interspecific interactions were relatively rare but during these interactions *T. vetulus* was always displaced by *S. entellus,* this resulted in the two species never occupying the same feeding trees at the same time. The majority of these interactions occurred during periods when fruit availability was low. Similar patterns of interaction have also been observed between *Pan troglodytes*, *Cercopithecus mitis*, *Cercopithecus ascanius* and *Lophocebus albigena,* where the dominance hierarchy among the four species corresponded to body weight (Houle et al. 2010).

However, the pattern of interaction observed in this study is in contrast to the interactions between *Semnopithecus johnii* and *Macaca silenus* (Sushma and Singh 2006) and between *Cercopithecus nictitans* and *Cercopithecus diana* (Eckardt and Zuberbuhler 2004), where the majority of the interactions were tolerant in nature. Such displacement interactions have been shown to promote coexistence between species through temporal niche partitioning, a situation where two or more species use the same resource at different times of the day (Ziv and Kotler 2003; Valeix et al. 2007). In the case of temporal niche partitioning, even though the dominant species depletes shared resources, coexistence is still possible if the two species have different foraging efficiencies. For example in the case of the nocturnal rodent *Gerbillus allenbyi* and *G. pyramidum* interference competition by *G. pyramidum* was shown to produce temporal niche partitioning between the two species (Ziv and Kotler 2003). In this case coexistence was shown to be possible as a result of *G. allenbyi* being energetically more efficient at foraging and being able to subsist on resource patches already depleted by *G. pyramidum* earlier in the night (Ziv and Kotler 2003). Thus, it is possible that though *S. entellus* displaced *T. vetulus,* that *T. vetulus* is an energetically efficient forager in comparison with *S. entellus* and is able to reuse food patches depleted by *S. entellus* and thereby coexists with *S. entellus* even during months when dietary overlap between the two species was extensive.

Interspecies interaction has been shown to impact the foraging behavior of numerous organisms (Ziv and Kotler 2003; Houle et al. 2010). In this study *T. vetulus* spent a lower proportion of time feeding when in close proximity to *S. entellus* in comparison with when the species was alone. Similar observations were also made in a study on a primate community in Uganda, in which *Cercopithecus mitis* reduced its foraging effort when in the presence of large bodied dominant species such as *Pan troglodytes, Cercopithecus ascanius* and *Lophocebus albigena.* Similarly, interference interactions were also shown to maintain the difference in the feeding patch size between *Varecia variegata rubra* and *Eulemur fulvus albifrons* (Vasey 2000) and *Saguinus mystax* and *S. fuscicollis* (Peres 1996). In the case of the rodents *Gerbillus allenbyi* and *G. pyramidum*, when *G. allenbyi* was together with *G. pyramidum,* the species depleted seed patches to a lower level in comparison with when it was in isolation, and also became more active later in the night to minimize contact with *G. pyramidum* (Ziv and Kotler 2003). Hence, it is possible that the reduced mobility and the high percentage of time devoted towards resting by *T.*

vetulus (Hladik 1977) is an adaptation by *T. vetulus* to minimize direct contact with *S. entellus*.

As with *S. entellus* and *T. vetulus* in this study, niche separation through vertical partitioning of a common habitat has been observed in many different primate communities (Charles-Dominique 1974; Ungar 1996; Sushma and Singh 2006; Buzzard 2006; Singh et al. 2011). Both *T. vetulus* and *S. entellus* at Kaludiyapokuna utilized all four vertical strata of the forest to different degrees. In general, *T. vetulus* at Kaludiyapokuna was highly arboreal and preferred the higher strata (L1 and L2) of the forest in comparison with *S. entellus*, which preferred the lower strata (L3 and L4) of the forest, but rarely used the ground (4.2% of observations). This behavior is contrary to the vertical habitat use patterns of *S. entellus* at other localities where the species in known to spend over 80% of the day on the ground (Bennett and Davies 1994). This difference in vertical habitat use by *S. entellus* in this study may be a behavioral response by the species to the presence of a full complement of terrestrial predators such as *Panthera pardus* and *Python molurus* at the Kaludiyapokuna study site. However, when the two species were in close proximity, during which *T. vetulus* was always displaced from feeding trees, *S. entellus* began to occupy the L2 stratum, the most frequently used stratum of the forest by *T. vetulus*. This resulted in *T. vetulus* occupying L2 less frequently than expected by chance. Similar observations were also made in a primate community in Uganda, where subordinate species preferred to feed in the tree crowns when in isolation but fed in lower strata of the forest when in the presence of dominant species (Houle et al. 2010). In this study, *S. entellus* was probably able to displace *T. vetulus* as a result of occurring in much larger groups in comparison with *T. vetulus*. The average group size for *S. entellus* and *T. vetulus* at Kaludiyapokuna was 15 and 7 animals per group respectively.

The results of this study are consistent with several of the proposed predictions, which suggest that interspecific competition influences the ecology and behavior of these primate species. The monthly fruit and flower overlap between the two species of primates in this study showed a high level of variation in relation to monthly availability of these resources. In comparison, monthly immature leaf overlap showed less variation in relation to immature leaf availability. The monthly variation in fruit overlap in relation to fruit availability was not consistent with the predictions based on competition theory. On the contrary, both species tended to utilize the same fruit tree species during periods of fruit scarcity. This resulted in high fruit overlap during those periods. This observation suggests that fruit is an important component of the diets of these colobine monkeys. The monthly variation in immature leaf overlap in relation to immature leaf availability was also not consistent with the predictions based on competition theory. However, the monthly variation in flower overlap in relation to flower availability was consistent with the predictions of competition theory. This observation should be interpreted with caution as flowers are an extremely ephemeral resource and observed patterns in monthly flower overlap may be a case of one or both species transitioning to alternative resources as the availability of flowers diminishes rather than the result of interference by one species on the other. However, the results of this study also show that interactions between *S. entellus* and *T. vetulus* occurred mostly during the period when fruit availability was low. These interactions resulted in a reduction in the proportion of time devoted to feeding by *T. vetulus*. In addition, during these interactions *T. vetulus* was displaced from feeding trees, which also resulted in *T. vetulus* altering its vertical habitat use pattern. These observations suggest that *S. entellus* is dominant over *T. vetulus* and hence it is possible that the low level of mobility and the comparatively high proportion of time devoted to resting reported for *T. vetulus* (Hladik 1977) and habitat and dietary niche partitioning by these species are strategies adopted by these primates to mitigate ecological competition and promote coexistence.

5.5 Bibliography

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5.6 Tables

Table 5.1. Composition of study groups. AM= Adult male, AF= Adult female, SA= Sub adult, JV= Juvenile, IN = Infant.

Species	AM	AF	SA	JV	IN	Total
S. entellus	3	7	3	7	2	22
T. vetulus	1	6	0	0	4	11

Table 5.2.Tree composition in the home ranges of two groups.

	S. entellus		*T. vetulus*	
Area sampled (ha)	1		0.48	
Number of species	48		30	
Number of families	24		19	
Stem density (stems/ha)	643		698	
DBH				
Mean (95% CI)	24.3 (22.5 26.1)		22.0 (20.0 24.0)	
Mode	9.0		9.0	
The 20 highest-ranking trees	Family	Species (BA/ha, relative BA/ha)	Family	Species (BA/ha, relative BA/ha)
	Ulmaceae	*Holoptelea integrifolia* (83968, 15.1)	Euphorbiaceae	*Drypetes sepiaria* (91747, 20.5)
	Euphorbiaceae	*Drypetes sepiaria* (76309, 13.7)	Moraceae	*Ficus microcarpa* (61443, 13.8)
	Moraceae	*Ficus microcarpa* (74749, 13.4)	Flacourtiaceae	*Hydnocarpus venenata* (51509, 11.5)
	Euphorbiaceae	*Mischodon zeylanicus* (35250, 6.3)	Euphorbiaceae	*Mischodon zeylanicus* (49218, 11.0)
	Flacourtiaceae	*Hydnocarpus venenata* (34182, 6.1)	Datiscaceae	*Tetrameles nudiflora* (23571, 5.3)
	Sterculiaceae	*Pterospermum suberifolium* (29648,5.3)	Ebenaceae	*Diospyros ebenum* (22982, 5.1)
	Annonaceae	*Diospyros oocarpa* (24023, 4.3)	Sterculiaceae	*Pterospermum suberifolium* (20978, 4.7)
	Datiscaceae	*Terameles nudiflora* (22628 4.0)	Sapindaceae	*Lepisanthes senegalensis* (14940, 3.3)
	Ebenaceae	*Diospyros ebenum* (14908, 2.7)	Fabaceae	*Dialium ovoideum* (13801, 3.1)
	Annonaceae	*Xylopia nigricans* (13477, 2.4)	Annonaceae	*Xylopia nigricans* (13718, 3.1)
	Lauraceae	*Cryptocarya sp.* (12019, 2.2)	Ebenaceae	*Diospyros oocarpa* (13101, 2.9)
	Sapotaceae	*Manilkara hexandra* (11615, 2.1)	Tiliaceae	*Grewia rothii* (10248, 2.3)
	Aponogetonaceae	*Wrightia angustifolia* (10333, 1.8)	Anacardiaceae	*Spondius dulcis* (8090, 1.8)
	Sapindaceae	*Lepisanthes senegalensis* (9518, 1.7)	Ebenaceae	*Diospyros ovalifolia* (7820, 1.8)
	Fabaceae	*Dialium ovoideum* (9448, 1.7)	Lauraceae	*Cryptocarya sp.* (5519, 1.2)
	Tiliaceae	*Grewia rothii* (8739, 1.6)	Ulmaceae	*Holoptelea integrifolia* (5115, 1.1)
	Sterculiaceae	*Pterygota thwaitesii* (8128, 1.4)	Sapindaceae	*Dimocarpus longan* (4801, 1.1)
	Euphorbiaceae	*Dimorphocalyx glabellus* (7117, 1.3)	Sapindaceae	*Lepisanthes tetraphyla* (4644, 1.0)
	Sapindaceae	*Dimocarpus longan* (6718, 1.2)	Aponogetonaceae	*Wrightia angustifolia* (4519, 1.0)
	Verbenaceae	*Vitex altissima* (6708, 1.2)	Aponogetonaceae	*Wrightia tomentosa* (3169, 0.7)

Table 5.3. Plant species shared by *S. entellus* and *T. vetulus* during each month of the study period and the contribution of each plant species to the monthly diets of the two primate species.

Month (Species)	*S. entellus* (% feeding time)	*T. vetulus* (% feeding time)
July		
Ficus microcarpa	6.17	11.84
Dialium ovoideum	5.05	35.53
Lannea coromandelica	0.75	10.53
Grewia rothii	0.56	3.95
Total	12.53	61.85
August		
Tetrameles nudiflora	27.45	15.22
Vitex altissima	19.96	1.73
Diospyros oocarpa	13.05	32.18
Wrightia angustifolia	8.06	2.08
Dialium ovoideum	4.22	2.42
Combretum ovalifolia	4.03	3.46
Hydnocarpus venenata	2.88	0.69
Holoptelea integrifolia	2.50	9.00
Ficus microcarpa	1.34	4.15
Pterospermum suberifolium	1.34	7.27
Democarpus longan	0.58	1.73
Lannea coromandelica	0.58	3.11
Total	85.99	83.04
September		
Tetrameles nudiflora	13.02	20.25
Mischodon zeylanicus	10.47	12.27
Drypetes sepiaria	7.21	7.98
Grewia rothii	6.74	0.61
Holoptelea integrifolia	6.51	1.23
Ficus microcarpa	5.81	17.18
Wrightia angustifolia	5.12	13.50
Combretum ovalifolia	5.12	3.07
Diospyros oocarpa	3.49	0.61
Hydnocarpus venenata	0.47	0.61
Total	63.96	77.31
October		
Grewia rothii	16.38	1.05
Lannea coromandelica	14.44	3.16
Hydnocarpus venenata	10.34	1.05
Wrightia angustifolia	8.19	2.11
Tetrameles nudiflora	3.45	3.16
Ficus microcarpa	3.02	25.26
Mischodon zeylanicus	2.80	3.16
Drypetes sepiaria	2.37	5.26
Mallotus eriocarpus	1.51	7.37
Commiphora caudata	0.65	11.58
Total	63.15	63.16

(*Continued*)

Table 5.3. (*Continued*)

November		
Grewia rothii	12.64	0.78
Tetrameles nudiflora	12.45	7.03
Mischodon zeylanicus	7.74	11.72
Ficus microcarpa	5.09	30.47
Commiphora caudata	1.51	17.97
Mallotus eriocarpus	1.13	1.56
Total	40.56	69.53
December		
Tetrameles nudiflora	24.41	18.66
Manilkara hexandra	19.41	1.49
Mischodon zeylanicus	17.35	20.15
Wrightia angustifolia	2.35	2.24
Ficus microcarpa	0.88	25.37
Commiphora caudata	0.59	22.39
Total	64.99	90.30
January		
Grewia rothii	36.82	12.24
Mischodon zeylanicus	16.89	23.47
Tetrameles nudiflora	14.19	22.45
Wrightia angustifolia	6.08	4.08
Lannea coromandelica	4.05	3.06
Manilkara hexandra	3.72	11.22
Total	81.75	76.52
February		
Drypetes sepiaria	43.33	11.04
Vitex altissima	16.63	5.19
Mischodon zeylanicus	11.60	35.06
Commiphora caudata	7.88	22.08
Wrightia angustifolia	2.84	9.09
Manilkara hexandra	1.75	7.14
Opilia amentacea	0.88	2.60
Lannea coromandelica	0.22	1.95
Ficus microcarpa	0.22	0.65
Abelmoschus angulosus	0.22	0.65
Total	85.57	95.45
March		
Drypetes sepiaria	50.14	27.27
Lepisanthus senagalensis	14.36	0.83
Ficus microcarpa	7.32	52.89
Dialium ovoideum	5.42	2.48
Mischodon zeylanicus	4.88	4.13
Combretum ovalifolia	0.81	7.44
Total	82.93	95.04
April		
Ficus microcarpa	16.39	9.09
Mischodon zeylanicus	14.72	7.95
Combretum ovalifolia	9.36	11.36
Xylopia nigricans	4.68	18.18
Tricalysia dalzelli	0.67	13.64
Total	45.82	60.22

(*Continued*)

Table 5.3. (*Continued*)

May		
Mischodon zeylanicus	38.21	29.27
Ficus microcarpa	19.81	9.76
Tricalysia dalzelli	4.25	9.76
Manilkara hexandra	3.77	18.29
Combretum ovalifolia	1.89	19.51
Total	67.93	86.59
June		
Drypetes sepiaria	54.07	49.09
Wrightia angustifolia	10.47	1.82
Tricalysia dalzelli	4.07	3.64
Combretum ovalifolia	3.49	40.00
Total	72.10	94.55

Table 5.4. Spearman correlation coefficients (r_s) values for plant item availability versus interspecies encounter rates.

Variables	r_s	$p \leq$
Fruit FAI vs Fruit overlap	0.098	0.762
Flower FAI vs Flower overlap	0.699	0.011*
Immature leaves FAI vs Immature leaf overlap	0.266	0.404

Table 5.5. Spearman correlation coefficients (r_s) values for plant item availability versus interspecies encounter rates.

Variables	r_s	$p \leq$
Fruit FAI vs Encounter rate	-0.670*	0.017
Flower FAI Flowers vs Encounter rate	0.356	0.256
Immature leaves FAI vs Encounter rate	-0.049	0.879

Table 5.6. Vertical habitat use patterns in *S. entellus* and *T. vetulus* when each species was not in close proximity to the other. Ex= Expected count; L1= 20-40 m; L2= 10-15 m; L3= 1-5 m; L4= 0 m.

Species			Habitat		
	L1 (Ex)	L2 (Ex)	L3 (Ex)	L4 (Ex)	Total (Ex)
S. entellus	114 (123.6)	361 (422.8)	148 (89.6)	27 (14.0)	650 (650)
T. vetulus	231 (221.4)	819 (757.2)	102 (160.4)	12 (25.0)	1164 (1164)

Table 5.7. Vertical habitat use patterns in *S. entellus* and *T. vetulus* when each species was in close proximity to the other. Ex= Expected count; L1= 20-40 m; L2= 10-15 m; L3= 1-5 m; L4= 0 m.

Species			Habitat		
	L1 (Ex)	L2 (Ex)	L3 (Ex)	L4 (Ex)	Total (Ex)
S. entellus	24 (51.4)	198 (183.2)	49 (39.4)	14 (11.0)	285 (285)
T. vetulus	96 (68.6)	230 (244.8)	43 (52.6)	12 (14.9)	381 (381)

Table 5.8. Monthly mean (range) dietary overlap values (percentage or simplified Morisita indeces (C_H)) between ecologically similar primate species. Fr= fruit overlap; Fl= flower overlap; Im= Immature leaf overlap; *= overlap estimated using C_H

Species	Monthly mean overlap (range)	Study site	Source
Colobus guereza vs *Procolobus dadius*	7.09 % (2.00-15.68)	Kibale, Uganda	Struhsaker and Oates (1975)
Colobus guereza vs *Procolobus dadius*	43.18 % (25.90-72.25)	Kibale, Uganda	Chapman et al. (2002b)
Trachypithecus vetulus vs *Semnopithecus entellus*	0.34 (0.00-0.98)^{Fr*}	Kaludiyapokuna FR, Sri Lanka	This study
	0.23 (0.00-0.92)^{Fl*}	Kaludiyapokuna FR, Sri Lanka	This study
	0.50 (0.15-0.89)^{Im*}	Kaludiyapokuna FR, Sri Lanka	This study
Alouatta guariba vs *A. caraya*	45.64 % (28.70-64.08)	El Piñalito PP, Argentina	Agostini et al. (2010)
Eulemur fulvus vs *E. rubriventer*	43% (6.50-66.00)	Ranomafana NP, Madagascar	Overdorff (1993)
Cercopithecus cambelli vs *C. diana*	73% (46-97)	Taï. Ivory Coast	Buzzard (2006)
Cercopithecus cambelli vs *C. petaurista*	59% (50-67)	Taï. Ivory Coast	Buzzard (2006)
C. petaurista vs *C. Diana*	65% (54-77)	Taï. Ivory Coast	Buzzard (2006)

5.7 Figures

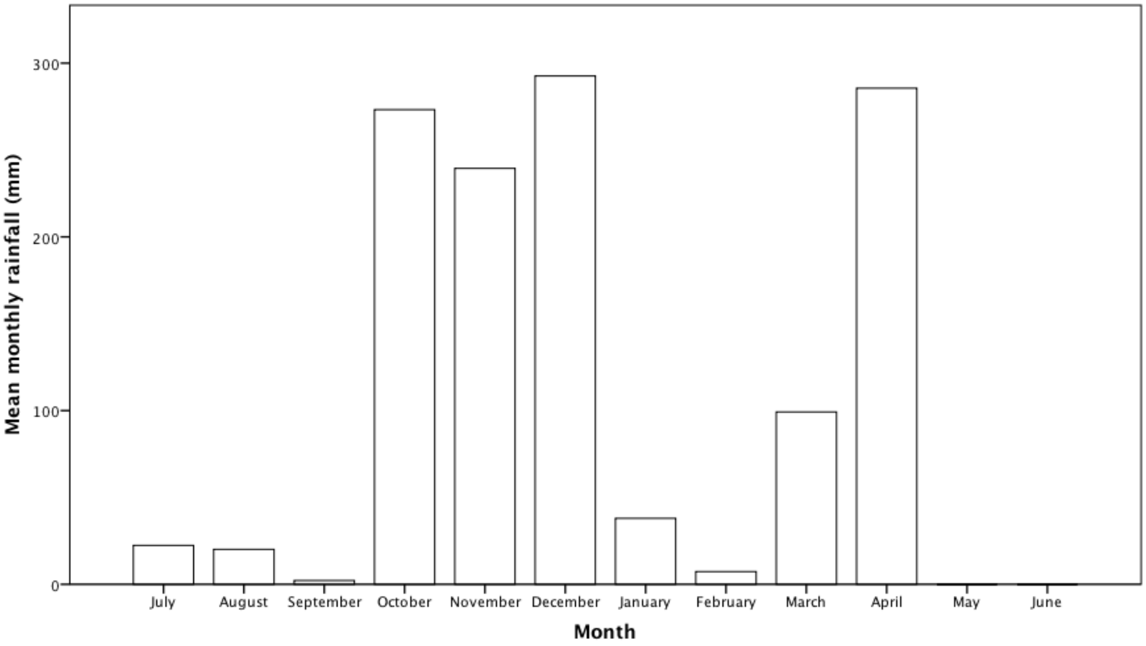

Figure 5.1. Rainfall pattern at Kaludiyapokuna during July 2008 to June 2009 showing peaks in October -December and March-April. Notably the driest months produced almost no rainfall.

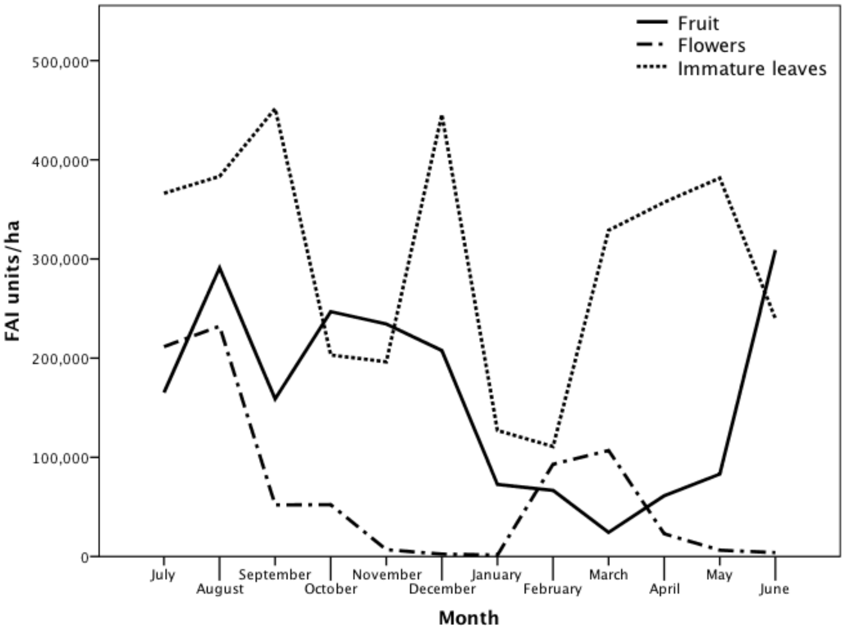

Figure 5.2. Monthly variation in fruit, flower and immature leaf availability in FAI units/ha in the study site from July 2008 to June 2009.

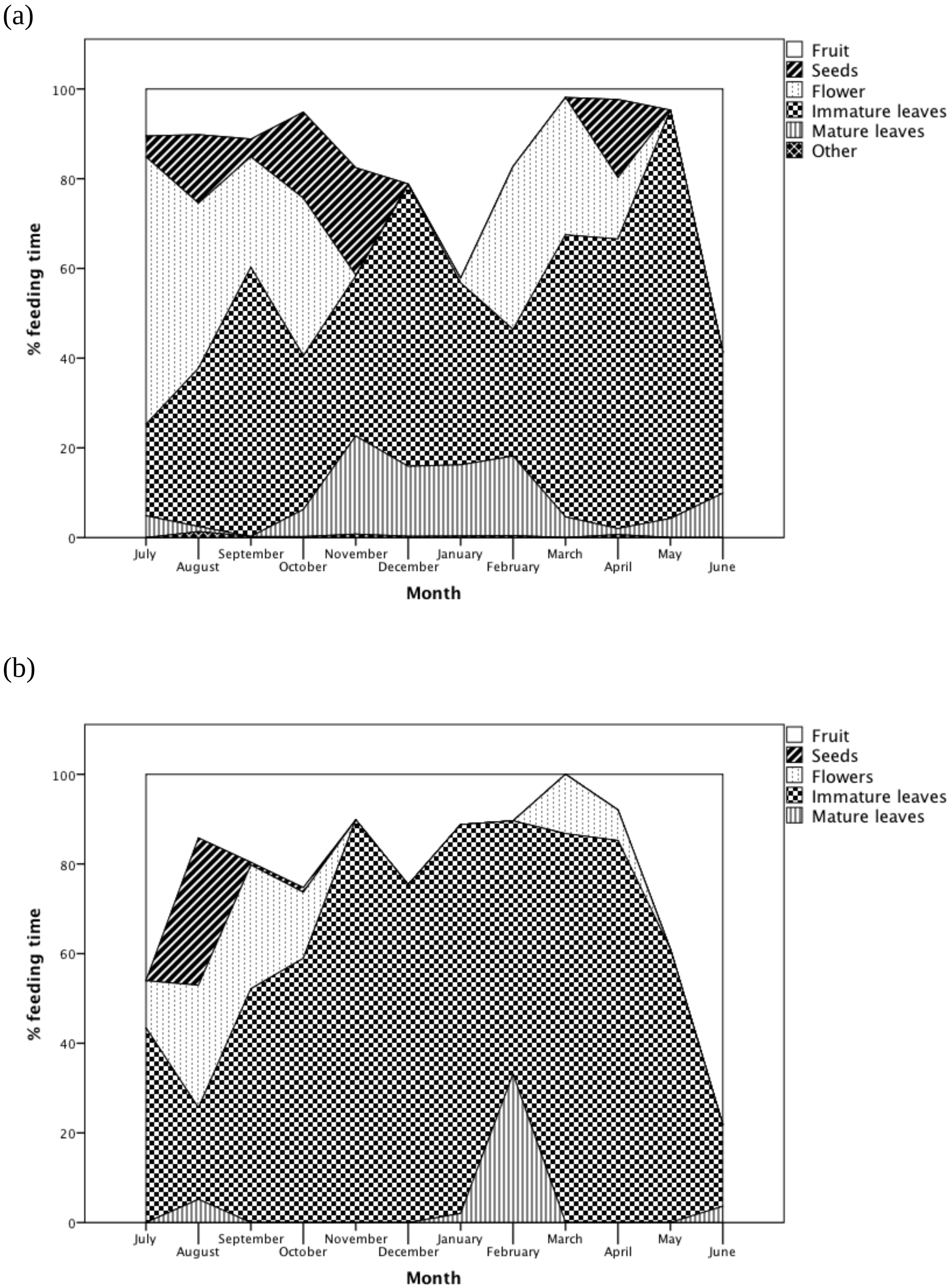

Figure 5.3. Monthly variation in the percentage of time devoted to feeding on different plant items by (a) *S. entellus* and (b) *T. vetulus* during the study period.

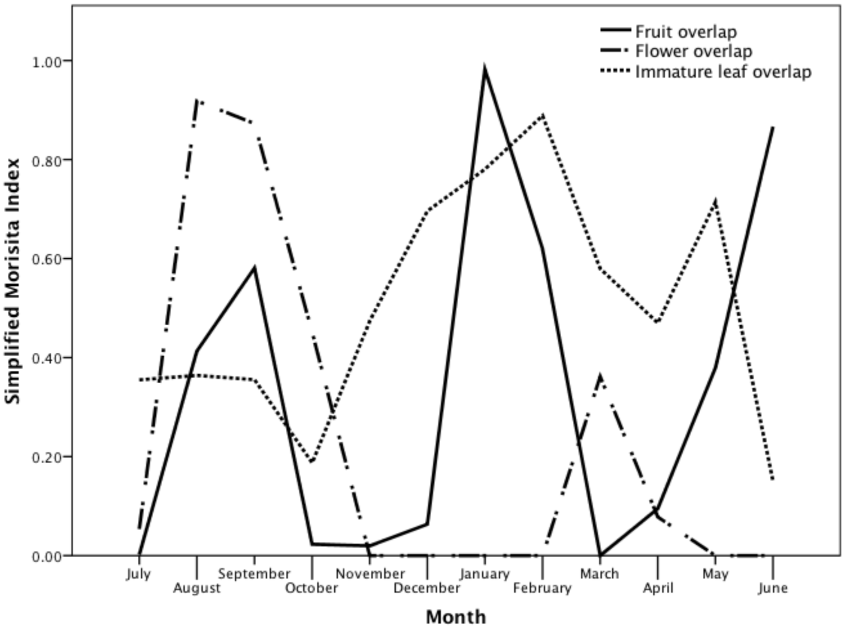

Figure 5.4. Monthly variation in ovelap in fruit, flower and immature leaves between *S. entellus* and *T. vetulus*. Note that fruit overlap is highest during the month of January when fruit availability was relatively low.

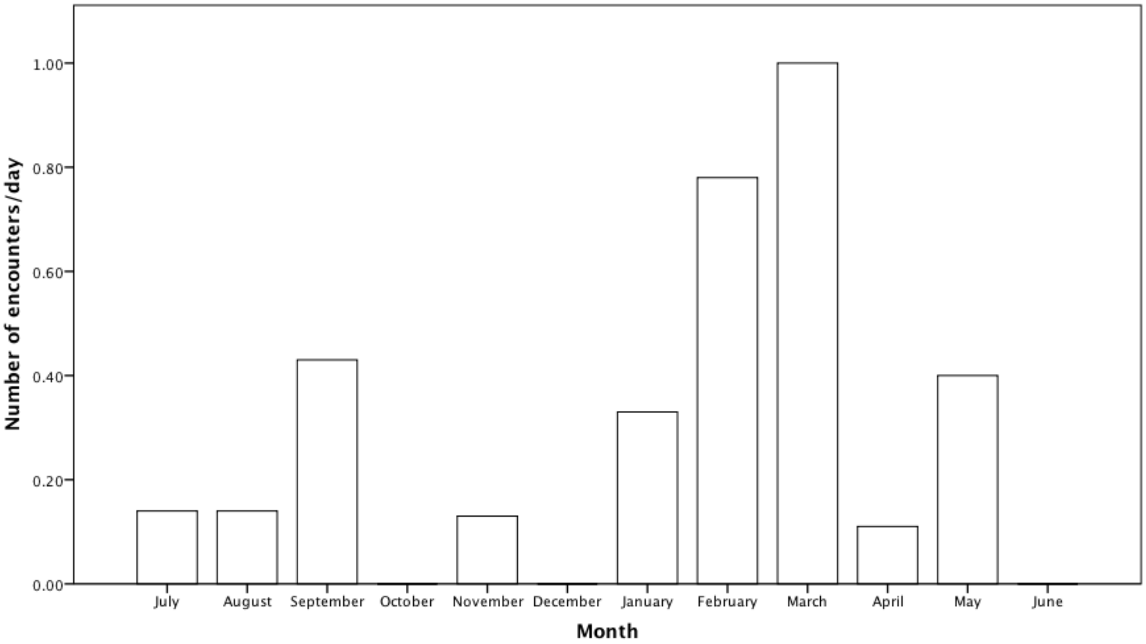

Figure 5.5. The frequency of incidents where *T. vetulus* and *S. entellus* were in close proximity during the study period in relation to fruit availability.

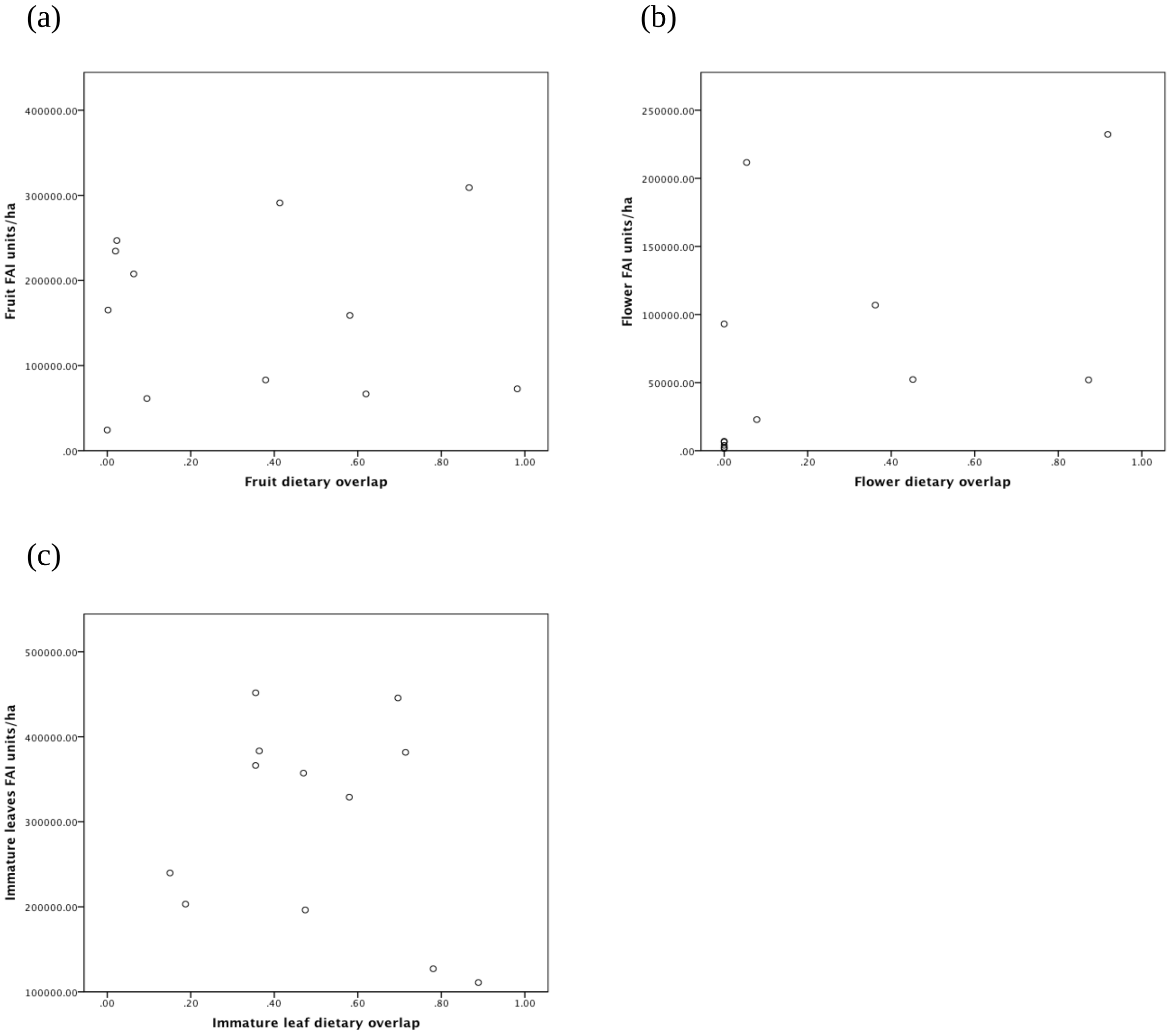

Figure 5.6. A visual representation of Spearman rank order correlations between monthly plant part availability *versus* monthly plant part dietary overlap. (a) Fruit availability vs % fruit dietary overlap (r_s= 0.098; p ≤ 0.762, (b) flower availability vs % flowers dietary overlap (r_s= 0.699; p ≤ 0.011) and (c) immature leaf availability vs % immature leaf dietary overlap (r_s= 0.266; p ≤ 0.404). These figures illustrate a correlation; these are not a regression and there is no intention of predicting the values of one axis from those on the other."

Chapter 6

Conclusions

Numerous studies on primate communities have identified niche differences that promote coexistence among primates (Hladik 1977; Buzzard 2006; Singh et al. 2011). However, precisely how these niche differences have evolved and how these differences are maintained ecologically over time is poorly understood. Studies on other plant and animal communities have shown that ecological interactions such as mutualism (van der Heijden et al. 1998; Stachowicz 2001), predation (Turner and Mittleback 1990) and ecological competition (Pacala and Roughgarden 1985) create niche differences among species in ecological communities. Of these interactions, interspecific competition has been shown to influence niche differentiation in numerous animal communities (Pacala and Roughgarden 1985; Ziv and Kotler 2003). However, in the case of primate communities, the broader role of interspecific competition in promoting and maintaining niche differences is poorly understood.

In this dissertation, I present data on the dietary ecology, ranging, habitat use and interspecific interaction in *Trachypithecus vetulus* and *Semnopithecus entellus,* two Asian colobine monkeys, to identify differences in certain aspects of the niches of these species and to assess the extent to which interspecific competition promotes and maintains these niche differences. The study was conducted at the Kaludiyapokuna forest reserve, a relatively undisturbed forest in the north central dry zone of Sri Lanka. The north central dry zone forests of Sri Lanka provided an ideal opportunity to study the interaction of these two species, which overlapped in their ranges in this region.

6.1 Comparative feeding ecology *S. entellus* and *T. vetulus*

In Chapter 3, I described the dietary ecology of *S. entellus* and *T. vetulus* at the Kaludiyapokuna forest reserve with the objective of identifying key differences in the dietary niches of these species and also to assess whether dietary differences reported for these species in previous studies could be generalized to this population. In addition, I quantified and defined the spatial distribution of key food resources utilized by these primates to determine if resource distributions enhance the potential for intraspecific and interspecific interactions in these primates.

In this study, all three groups allocated different proportions of feeding time to feed on different dietary items. The monthly variation in the proportions of times allocated to feeding on fruits and immature and mature leaves by the three groups was not statistically significant. This finding is contrary to the findings of other studies on sympatric populations of these primates, where *S. entellus* was shown to include high proportions of seasonal plant parts (fruits and immature leaves) in its diet, while *T. vetulus* was shown to be extremely folivorous and include a higher percentage of mature leaves in its diet year-round. Both species fed on fruit and flowers according to their availability at the study site, but did not consume immature leaves according to their availability. These results indicated that both species preferred to feed on fruits and flowers over leaves, a trend that has not been observed for these species in the past. This population of langurs also consumed a high proportion of flowers in comparison to other colobine populations, making this population one of the most florivorous colobine populations. In addition, both species preferred to feed on tree species that were relatively rare and showed clumped distributions. Clumped resource distributions have been suggested to promote within-group and interspecific competition. However, alternative hypotheses such as the resource dispersion hypothesis (RDH) suggest that clumped resources do not necessarily promote competition among animals living in social groups. These results indicate that the dietary ecology of *T. vetulus* and *S. entellus* at Kaludiyapokuna is extremely similar and the mechanism proposed to explain the coexistence of the two species at Polonnaruwa, which suggests that coexistence between these two species is possible because *T. vetulus* is adapted to subsisting on a diet low in nutritional value is not directly applicable to this population. Hence, alternative mechanisms such as differential giving up densities (GUD), which combines optimal patch use from optimal foraging theory with mechanisms of coexistence from resource theory, should be considered. This mechanism proposes that even if two species have identical resource use patterns, coexistence is still possible if the two species have different foraging efficiencies. Additionally, the results of this study together with previous findings on these species indicate that these colobine species are flexible in their dietary ecology, and dietary variation reported for these species is driven by local ecological conditions.

6.2 Ranging behavior of *S. entellus* and *T. vetulus*

In Chapter 4, I decribed the ranging behavior of *S. entellus* and *T. vetulus* with the aim of identifying differences in the ranging behaviors of the two species and also provide insight into how these differences might facilitate coexistence. In addition, I also explored the relationship between group size, food availability and ranging behavior.

All three groups occupied habitats that were similar in terms of abundance of plant species. In the case of *S. entellus* Groups A and B, the home range of Group A was larger then Group B. This difference in home range size probably reflected the higher energetic demand of Group A, which was twice as large as Group B. The home ranges of *S. entellus* in this study were the smallest reported for the species. In comparison, the home range of *T. vetulus* in this study was much larger than previously reported. The home range overlap between the two species was also extensive and was similar to the situation between these two species at Polonnaruwa. The daily path length of Group A was longer than the daily path lengths of Group B and *T. vetulus*. The longer daily path length of Group A probably reflected the increased energetic demands of the members of the group. The average daily path length of Group A was also influenced by fruit availability. Group A tended to travel more during periods of fruit scarcity. This pattern is contradictory to the ranging behavior of some species of colobines, which have been shown to increase their daily travel distance during periods when the diet was dominated by fruits and flowers rather than by leaves. In the case of Group B and *T. vetulus*, the results indicated that the two species did not alter their ranging behavior in response to resource availability in a similar fashion to Group A. These observations together with other published works on colobine ranging behavior suggest that no one particular foraging strategy can categorize the behavior of a species.

The intensity of home range use, defined as index of defendability (*D*) was higher for *S. entellus* in comparison with *T. vetulus*. The index of defendability (*D*) compares average day length in relation to the diameter of a circle with an area equal to the observed home range. A high *D* value implies frequent contact with home range boundaries at widely separating points on the perimeter is indicative of intense home range use, and a high degree of territoriality. The low *D* for *T. vetulus* indicates that *T. vetulus* travelled a relatively short distance on any given day in comparison with *S. entellus* and consequently utilized only a fraction of its total home range. This behavior is consistent with the behavior of *T. vetulus* at Polonnaruwa and probably reduces direct contact with *S. entellus* and promotes temporal niche partitioning, a situation where the two species can utilize shared areas of their home ranges at different times and ultimately reduce ecological competition. The low defendability (*D*) observed for *T. vetulus* in this study also contradicts the behavior of *T. vetulus* at Polonnaruwa, where the species has been reported to be extremely territorial. The low defendability (*D*) for *T. vetulus* in this study is possibly the result of the relatively low density of the species at the study site (19 animals/km^2) in comparison to Polonnaruwa (100-200 animals/ km^2). The low density of conspecifics probably alleviated the need for the *T. vetulus* group to regularly traverse its entire home range to monitor and deter other conspecific groups from intruding. Conversely, the relatively high population density of *S. entellus* at the study site (53 animals/ km^2) probably required Groups A and B to regularly traverse their home ranges to deter potential intrusion from conspecific groups, which probably resulting in a comparatively higher index of defendability (*D*).

6.3 Dietary overlap, habitat use and interspecific interaction in *S. entellus* and *T. vetulus*

In Chapter 5, I presented data on dietary overlap, vertical habitat use and interspecific interactions. In this chapter, I specifically explored the monthly variation in dietary overlap in relation to monthly resource availability and the influence of interspecific interaction of foraging efficiency and vertical habitat use to determine if differences in the dietary ecology and ranging behavior observed for these species in this study have evolved in response to interspecific competition. The data on diet overlap, habitat use and interspecific interaction were used to test the four predictions outlined in Chapter 1.

The dietary overlap between *S. entellus* and *T. vetulus* showed considerable temporal variation in comparison to dietary overlap between other closely related primate species. However, the monthly differences between fruit, flower and immature leaf overlap were not statistically significant. Average immature leaf overlap was the highest between these primate taxa, followed by fruit and flower overlap. In this study, the monthly variation in fruit overlap in relation to fruit availability was not consistent with the first prediction, which predicted that dietary overlap should be high during periods of resource abundance and low during periods of resource scarcity. Contrary to the prediction, during periods of fruit scarcity, both species began to utilize the same fruit tree species, which resulted in high fruit overlap during periods of fruit scarcity. The monthly variation in immature leaf overlap in relation to immature leaf availability was also not consistent with the predictions of the first hypothesis. However, the monthly variation in flower overlap in relation to flower availability was consistent with the the first prediction.

The results of the study also show that interaction between the two primate species were infrequent. Most interactions that did occur happened during periods when fruit availability was low. This observation was consistent with the second prediction, which predicted that the rate of interspecific interaction should be high during periods of resource scarcity. These interactions resulted in a reduction in the proportion of time devoted to feeding by *T. vetulus*, which was consistent with the third prediction, which predicted that the feeding efficiency of one or both species should decline as a result of interspecific interactions. During these interactions *T. vetulus* was displaced from feeding trees and this resulted in *T. vetulus* altering its vertical habitat use pattern. This outcome is consistent the fourth prediction, which predicted that one of the two species, should displace and alter the habitat use pattern of the other during interspecific interactions. These finding suggests that *S. entellus* is ecologically dominant over *T. vetulus* and influences certain aspects of the behavior of *T. vetulus*. In this study, *S. entellus* was probably able to displace *T. vetulus* as a result of occurring in much larger groups in comparison to *T. vetulus*. Thus, the system of low mobility strategy adopted by *T. vetulus* and reluctance shown by the species to feed on trees with *S. entellus* at the same time are probably behavioral adaptations by *T. vetulus* to minimize direct interaction with *S. entellus* and facilitate coexistence.

6.4 Future directions

Overall, the results of this study suggest that interactions between *T. vetulus* and *S. entellus* influenced the feeding and habitat use patterns of *T. vetulus*. However, it should be noted that the study involved only a limited number of groups and hence, whether the findings of this study could be generalized to other groups of these species needs to be explored. In addition, a number of studies have shown primates within a particular study site alter their diets over longer temporal scales in response to changes in the floral structure of the habitat. Hence, the intensity of interspecific interactions may also change over longer temporal scales. To address some of these issues, attempts will be made to habituate and collect behavioral and ecological data from additional *T. vetulus* and *S.*

entellus groups in the future. In addition, efforts will be made to continue data collection on the currently habituated groups so that questions relating to changes in diet and the intensity of competition over longer temporal scales could be addressed. To further investigate the influence of interspecific interaction on the ecology of these primates, studies will also be conducted on allopatric populations of *T. vetulus* and *S. entellus* and the observations will be compared to those from sympatric populations. In addition to this, alternative mechanisms of coexistence such as differential giving up densities (GUD), which combines optimal patch use from optimal foraging theory with mechanisms of coexistence from resource theory, will be tested to elucidate mechanisms that enable these primates to coexist (Ziv and Kotler 2003). This model proposes that even if two species have identical resource use patterns coexistence is still possible if the two species have different foraging efficiencies. Thus, it is possible that though *S. entellus* and *T. vetulus* in this study showed similar resource use patterns, and *S. entellus* displaced *T. vetulus* from feeding trees, that *T. vetulus* is an energetically efficient forager in comparison with *S. entellus* and is able to reuse food patches depleted by *S. entellus* and thereby coexists with *S. entellus* even during months when dietary overlap between the two species is extensive.

6.5 A note on the conservation of *T. vetulus* and *S. entellus*

At present, *T. vetulus* and *S. entellus thersites* are listed as endangered in the IUCN Red List of Threatened Species and habitat loss has been identified as the major cause for their decline (IUCN 2011). Major development projects initiated by the government of Sri Lanka have contributed significantly to the deforestation of dry zone and other regions of Sri Lanka. In addition, traditional agricultural methods such as short-rotation swidden agriculture, intensive cattle grazing and the conversion of forests into agricultural plantations have contributed significantly to deforestation in Sri Lanka (Perera 2001). The cultivation of tea, rubber, coffee, coconut or other permanent crops and other types of timber harvesting has resulted in a 68% reduction in natural high forest cover between 1900 and 1983 (Perera 2001). Apart from these factors, natural phenomena such as cyclones also cause damage to forests, especially in the dry zone (Dittus 1985). All these factors have contributed to an annual deforestation rate of 3.5%, which places Sri Lanka as the country with the highest rate deforestation in Asia (Dinerstein and Wikramanayake 1993). Although approximately 12% of the land cover of Sri Lanka has been designated as protected areas, it has been predicted that habitat loss will continue to occur outside the protected areas, and this will compromise the survival of primates and other wildlife that reside outside the protected area network (Dinerstein and Wikramanayake 1993). This is particularly a concern for two subspecies of *T. vetulus*, *T. vetulus nestor* and *T. vetulus vetulus*, which occupy habitats such as home gardens that are outside the protected area system (IUCN 2011). Low-level subsistence hunting of *S. entellus* and *T. vetulus* has been reported (IUCN 2011) but is unlikely to have a major impact on the long-term survival of these species.

The management of protected areas in Sri Lanka is also problematic. The protected areas designated as National Parks are managed by Department of Wildlife Conservation while protected areas designated as Forest Reserves are under the purview of the Forest Department of Sri Lanka. In addition, sections of forests within these protected areas are often managed by the Department of Archaeology of Sri Lanka due to the presence of archaeological ruins within these forests. The Department of Archaeology reserves the right to clear these forests to aid excavation or to improve access to these archeological sites even if this is detrimental to the flora and fauna of the reserve.

Considering the present plight of these primates, urgent national measures are necessary to ensure the longterm survival of these primates in Sri Lanka. The management of habitats outside the protected area network needs to be addressed urgently. In addition, the management structure of protected areas needs to be critically reviewed. It is hoped that this study will generate an interest in the ecology of *S. entellus* and *T. vetulus* in Sri Lanka and motivate conservation measures for these species.

6.5 References

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