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The Socioecology of Red-shanked Doucs (Pygathrix nemaeus) in Son Tra Nature Reserve, Vietnam

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THE SOCIOECOLOGY OF RED-SHANKED DOUCS (*PYGATHRIX NEMAEUS*) IN SON TRA NATURE RESERVE, VIETNAM

by

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written by Larry Ray Ulibarri
has been approved for the Department of Anthropology

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Professor Michelle Sauther

Professor Emeritus David Armstrong

Professor Barth Wright

Date ____________________

The final copy of this thesis has been examined by the signatories, and we find that both the content and form meet acceptable presentation standards of scholarly work in the above mentioned discipline.

Ulibarri, Larry Ray (Ph.D., Anthropology)

Title: The socioecology of red-shanked doucs in Son Tra Nature Reserve, Vietnam.

Dissertation directed by Professor Herbert Covert

Abstract

This study aimed to gather socioecologic data on the red-shanked doucs (*Pygathrix nemaeus*) in Son Tra Nature Reserve, Vietnam, over 16 months for the purposes of assisting conservation initiatives of the government of Da Nang City. This included the study of social organization, structure, size, ranging behaviors, activity budget, food choice, selectivity, and dietary quality. These data were compared to transect phenology and weather data.

The doucs live in modular societies with stable groups composed of stable units. The average group size was 18 individuals. Groups consisted of an average of 2.7 units with a daily pattern of fission-fusion. The degree of fission-fusion significantly correlates to daily activity budgets, leaf flush, and precipitation. Units always fused overnight. Average unit size was 6.5 individuals. Units were one-male/multi-female and multi-male/multi-female. Adult male to adult female sex ratio was 1:1.63 individuals, and young to adult ratio was 1:1.26 individuals. Home range was 36 ha with a core area of 8 ha. The average daily path length was 509 m, and path length was significantly and negatively correlated with precipitation. Social structures and organization are partly influenced by intergroup contest competition intensified by living in modular societies, ecological constraints including habitat quality and fragmentation, predation, and intragroup scramble competition.

The activity budget of all individuals showed that inactivity was most common (35.3%), followed by moving (28.6%), socializing (21.7%), feeding (13.7%) and self-grooming (0.7%). There are a few significant differences in activity budgets between seasons and groups of individuals, but more compelling is the relationship between the daily activity budget and the daily pattern of fission-fusion between units. When units are fused they rest significantly more, and when fissioned they move, feed, vocalize, and are vigilant significantly more. This pattern appears to be an adaptation to avoiding intragroup scramble competition and for maintaining contact and coordination between dispersed foraging units. The need for inter-unit coordination may relate to intergroup contest competition and resource defense. The high degree of vocalizations also may relate to intragroup coordination and intergroup contest competition.

The feeding budget of all individuals showed that leaves were most frequently selected (87.8%), followed by fruits and seeds (10.2%), flowers (1.6%) and bark/pith (0.4%). Young leaves were selected over mature leaves (68.6%), and whole leaf blades (86.5%) and petioles (13.1%) were more commonly selected leaf parts. Important food species on Son Tra include *Parashorea stellata*, *Parsonsia laevigata*, *Ipomoea eberhardtii*, *Garcinia morella*, *Ficus variegata*, *Ficus depressa*, and *Ancistrocladus tectorius*. Dietary diversity is low. Young leaves, and fruit and seeds, were not selected according to availability, suggesting that the doucs are selective foragers. Chemical and nutritional content of selected and non-selected leaves, and selected young and selected mature leaves, were not significantly different. The high quality of mature leaves might contribute to the high degree of folivory, suggesting a lack of dietary stresses.

These data have been helpful in the planning and implementation of various exhibitions, reforestation efforts, and the building of canopy bridges for the doucs to cross between habitat fragments on Son Tra Nature Reserve.

To Ulrike, my wife
and
Cheridee and Steve, my parents

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Chapter 1. Introduction and research aims

1.1. Introduction

The purpose of this study is to document, analyze, and compare the socioecology of red-shanked doucs (*Pygathrix nemaeus*) on Son Tra Nature Reserve, Da Nang City, Socialist Republic of Vietnam (hereinafter referred to as Vietnam). This involves analyses of group size and composition, ranging, activity budgets, diet, and seasonality. Through these analyses, this study seeks to contribute to conservation efforts on Son Tra Nature Reserve. The significance of this study to anthropology includes expanding our knowledge of red-shanked doucs, the genus *Pygathrix*, and Asian colobine ecology more generally.

Studies of non-human primates are a central theme in anthropology. Adaptations of extant primates are used to interpret the fossil record, such as analyses of diet (Covert & Kay, 1981; Kay & Hiiemae, 1974; Kirk & Simons, 2001; Ramdarshan et al., 2010), the evolution of locomotion in anthropoid and Eocene primates (Covert, 1988; Covert, 1995; Ryan et al., 2012a), the evolution of visual systems (Ankel-Simons & Rasmussen, 2008; Heesy & Ross, 2001; Stephenson, 1972), life history and plasticity in relation to environmental factors (Buck et al., 2010; Franzen et al., 2009; Sauther & Cuozzo, 2012; Stock & Buck, 2010), among others. Studies draw comparisons between extant non-human primates and hominids, including relationships between diets and morphology or niche partitioning (Aiello & Wheeler, 1995; Lee-Thorp et al., 2003; Peters et al., 1981; Teaford & Ungar, 2000; Ungar & Sponheimer, 2011).

Comparisons between extant and extinct forms are possible because numerous anthropologic and primatologic studies evaluate relationships between non-human primates and their environments (Fleagle, 2013), including feeding, locomotion, social organization, body size, gut morphology, skeletal morphology, color vision, ecosystem health, seed dispersal and flower pollination, among numerous others. Feeding ecology, in particular, has been central themes in anthropology and primatology. These studies examine relationships between feeding behavior and phenology (Brugiere et al., 2002; Chapman & Chapman., 1999; Dasilva, 1994; Milton, 1980), nutritional ecology (Janzen, 1978; Lambert, 2011; McKey, 1978; Oftedal et al., 1991), social relationships (Grueter & van Schaik, 2010; van Schaik, 1989), group sizes (Garber, 1987; Snaith & Chapman, 2007; Wrangham et al., 1993), variation in ranging (Chapman, 1988; Harrison, 1983; Milton & May, 1976; Tan, 1999; Williems et al., 2009), immune systems (Coe et al., 1992; McDade, 2003, Nikolich-Zugich & Messaoudi, 2005), polyspecific relationships (Chapman & Chapman, 1996; Garber, 1988; Noe & Bshary, 1997; Wachter, 1997; Waser, 1982), reproductive success (O'Toole et al., 1974; Sauther, 1998), ecosystem health (Bourliere, 1985; Chapman, 1989; Russo & Chapman, 2011; Lambert & Garber, 1998), and behavior and morphologies (Davies & Oates, 1994; Davies et al., 1999; Dominy & Lucas, 2004; Hohmann et al., 2006; Fashing, 2007), among others.

Of the 420 extant primate species and subspecies compiled by the *IUCN Red List of Threatened Species* (356 full species following Groves, 2001a), 42 are listed as Critically Endangered, 85 as Endangered, 79 as Vulnerable, and 23 as Near Threatened (IUCN, 2012). This means that 229 of 420 primate taxa (54.5%) face the risk of extinction, with an additional 56 (13.3%) that may be threatened but are classified as Data Deficient. The principal threats to the survival of these primates are anthropogenic, including hunting, habitat disturbance, loss, and fragmentation. Many consider the anthropogenic effect to be the principal force driving the current extinction rate. As illustrated by E.O. Wilson (1988; 1992), current extinction rates are 1000 to 10000 times higher than they were before human intervention. These results remain supported by various studies, despite scholarly debate (Stork, 2010, and references therein).

Many primate species are adapted to forests that have begun to disappear and change as result of human impacts. For species on the precipice such as the doucs, understanding these adaptations and behaviors in the wild is both a means to preventing local and global extinction, and a contribution to understanding primate evolution and the adaptive radiation of colobines.

The Colobinae is an adaptive radiation that is less studied than the Cercopithecinae, the other subfamily of Old World monkeys. Colobines represent a diverse radiation, including 59 species and 10 genera, 16.6% of the 356 extant primates (Groves, 2001a; Groves, 2001b; Groves, 2007a; Groves, 2007b). As detailed by Fashing (2011) and Kirkpatrick (2011), they are found on two continents, from sea level to 4500 m, in temperate to tropical environments, and in a wide range of forest types. They have various skeletal and physiological adaptations for moving within their environments, and employ a wide range of locomotor patterns from terrestrial and arboreal quadrupedalism to semi-brachiation. They form various flexible social groups, which may be environmentally adaptive as opposed to species-specific. Their diets are seasonal and varied, and include bark, insects, nuts, flowers, fruits, leaves, lichen, and seeds. They have various forms of ingestive and digestive adaptations. This adaptive suite is flexible, with some colobine species employing different behaviors over various seasons or environments. Despite the range and flexibility of this adaptive radiation, hunting and habitat loss have resulted in 48 of the 56 colobine species (85.7 %) being listed as threatened by IUCN (2013), including nine Critically Endangered, 20 Endangered, 12 Vulnerable, seven Near Threatened, and one listed as Data Deficient.

Among the Colobinae, *Pygathrix* was considered one of the least studied genera (Bennett & Davies, 1994). This genus contains three species: red-shanked douc, grey-shanked douc (*P. cinerea*) and black-shanked douc (*P. nigripes*). The grey-shanked and black-shanked doucs have recently been the subjects of long-term studies, and the red-shanked doucs are now represented with nearly 40 years of various captive and a few wild studies, adding to our knowledge of the genus. Captive studies cover a range of topics from feeding and locomotor behavior, infant-mother relationships, reproduction, morphology of hard and soft tissues, and systematic evaluations (see Benirschke, 2008; Brockman & Lippold, 1975; Byron & Covert, 2004; Darawiroj et al., 2012; Kulcharoen & Utara, 2010; Lippold, 1981; Ruempler, 1998; Wright et al., 2008a). Only a few studies have been conducted in the wild for any *Pygathrix* species. Until 2007, the only such study was published by Lippold (1977), based on 36.6 hours of observation over 2.5 months on red-shanked doucs at Son Tra. The last half decade has seen a tremendous increase in our understanding adaptations of *Pygathrix* from wild studies. This includes long-term wild studies on the black-shanked and grey-shanked doucs (Hoang Minh Duc, 2007; Ha Thang Long, 2009; Rawson, 2009), and field studies on red-shanked doucs (Phiapalath, 2009, Phiapalath et al., 2011; Dinh Thi Phuong Anh et al., 2010). This research adds a long-term study on the red-shanked doucs in the wild.

Species of *Pygathrix* are found only in Indochina and all have limited geographic ranges, being confined to the shrinking forests of the Annamite Mountains. Vietnam is the only country where all three species of *Pygathrix* occur. Red-shanked doucs are currently the only *Pygathrix* species reported from three Indochinese countries (central Vietnam, northeast Cambodia and central Lao People’s Democratic Republic, hereinafter referred to as Laos).

Vietnam has 24 primate taxa of six genera (Nadler et al., 2003; Nadler et al., 2007), of which about 92% (22 taxa) are threatened (IUCN, 2012; Nadler et al., 2007), including six Critically Endangered, nine Endangered, six Vulnerable, and one Near Threatened. Forests are being removed for timber and development (Sterling et al., 2006; Wege et al., 1999). Hunting and wildlife trade remains high despite legal protection (Li Yiming & Li Dianmo, 1998; Wenting Liu et al., 2008; Nadler et at., 2003). *In -situ* conservation efforts are often inadequate (Sterling et al., 2006), but current research efforts are taking strides to combine research and *in -situ* and *ex -situ* conservation efforts (see Covert et al., 2008; Ha Thang Long, 2009; Hoang Minh Duc, 2007; Workman, 2010). One important relationship between research and *ex -situ* conservation is the need for more detailed feeding ecology information in order to provide more appropriate foods to captive doucs. Captive doucs have been kept with little success in most locations except for the Endangered Primate Rescue Center in Vietnam, Singapore Zoo, and Bangkok Zoo, dying frequently of complications related to food and digestion (Lippold, 1993; Lippold, 2004; Ruempler, 1998). Relationships between research and *in -situ* conservation and protection efforts are direct, with information gathered and shared with governing bodies for enhancing the protection of the primates and their environments

All *Pygathrix* species are threatened with extinction; the grey-shanked douc is listed as Critically Endangered, and the red-shanked and black-shanked doucs are listed as Endangered (IUCN, 2013). Reasons for their reduced distribution and threatened status result from anthropogenic effects of hunting, trade, habitat loss and fragmentation (Lippold & Vu Ngoc Thanh, 1998; Nadler et al., 2003). A patchwork of protected areas remains the last refuge for many isolated and often remnant populations, including a population located in Son Tra Nature Reserve. This small reserve contains one of the largest remaining populations of red-shanked doucs in Vietnam (Lippold & Vu Ngoc Thanh, 2008). It is an important population because it is one of the largest remaining, and it has significant public awareness potential because it is located adjacent to a major city and tourist hub: Da Nang. It is currently the only location where people can observe red-shanked doucs in the wild reliably. This is partly due to the small area and the high degree of habitat fragmentation caused by road construction and tourism development on the peninsula. Habitat loss for resort development and fragmentation through road construction is the primary anthropogenic effect threatening biodiversity on Son Tra. Tutin and White (1999) suggested these anthropogenic effects have influenced primate populations for decades and their effects on natural behavior must be considered in any study. This concern is echoed often in various wildlife and environmental studies (Cantu-Salazar & Gaston, 2010; Godfrey & Irwin, 2007; Michalski & Peres, 2005; Morrison et al., 2007; Riley, 2007; Tutin, 1999). In light of this consideration, data gathered on Son Tra and the doucs remain applicable to analyses of adaptations of wild primates and results are comparable to current studies.

1.2. Research aims

The aim of this study is to understand the adaptive niche of the red-shanked doucs on Son Tra Nature Reserve including the foods they eat, the foods which are available, nutrient and chemical values of select foods, ranging distances, sizes, and patterns, group organization and composition, activity budgets, and the influences of seasonality (weather and phenology) on the above factors. There were three broad categories of questions with 11 associated hypotheses that guided initial data collection.

1.2.1. Concerning social structure/organization

Do red-shanked doucs primarily live in one-male units or will multi-male units be regularly encountered? What is group size and sex ratio? If the doucs follow a seasonal or daily fission-fusion pattern, is this influenced by food availability or weather? What is ranging behavior like on Son Tra, and how does this vary according to season, resource availability or weather? If certain social behaviors such as mating, aggression, parental care, and allomothering are observed, how are they expressed and what variables influence their occurrence or seasonality?

Among Asian colobines the one-male unit tends to be the central social unit, although there are variations on this theme (Kirkpatrick, 2011). Black-shanked and grey-shanked doucs have been reported to live in various social units including one-male units, multi-male units, bands of one-male units, all male units, and single individuals (Hoang Minh Duc, 2007; Ha Thang Long, 2009; Rawson, 2009). For red-shanked doucs, it has been reported that one-male units and multi-male units form bands with a daily fission-fusion pattern (Dinh Thi Phuong Anh et al., 2010), and they live in multi-male multi-female groups (Lippold, 1977; Lippold, 1998). However, there is little information about the degree and patterns of unit cohesion and what factors influence its occurrence. Home ranges among black-shanked doucs are reported to vary between 20.1 and 50 ha (Hoang Minh Duc, 2007; Rawson, 2009). For other colobines home ranges can vary from a mere handful of ha (Fuentes, 1994; Hladik, 1977; Watanabe, 1981) up to 3,500 ha (Bleisch et al., 1993).

> ***Hypothesis 1a*** – Group structure among doucs is multi-male resulting from unit fusion and the less frequent occurrence of multi-male units. Units will have a 1:2 male to female ratio as has been reported among most colobines and *Pygathrix* studies (Chapter 2), regardless if the unit is one-male or multi-male.
>
> ***Hypothesis 1b*** – The doucs will exhibit a daily fission-fusion pattern as reported by Dinh Thi Phuong Anh et al. (2010). Considering this is a daily pattern, there will be no seasonal change; therefore this is not affected by resource availability or weather patterns.

Hypothesis 1c – Patterns of ranging will be influenced by resource availability and/or weather, with daily path lengths and variation in the use of home range significantly increasing during resource scarcity and/or drier and warmer weather.

1.2.2. Concerning activity budget

What is the activity budget of the red-shanked doucs? How does this compare to other *Pygathrix* studies and colobines? Do activity budgets vary significantly between males and females? If so, does resource availability or weather variables account for this variation? To what degree do activity budgets vary seasonally, and to what degree can this variation be attributed to measured external variables?

For *Pygathrix*, studies on the black-shanked doucs follow typical colobine activity patterns of high inactivity/resting, followed by feeding (Hoang Minh Duc, 2007; Rawson, 2009). However Ha Thang Long (2009) reported the grey-shanked doucs deviate from this pattern: resting is still high but traveling and socializing each account for a greater proportion of time than does feeding. Seasonal differences also tend to follow typical colobine patterns, with increases in resting during the wet season, and increases in feeding and traveling during the dry seasons (Hoang Minh Duc, 2007; Ha Thang Long, 2009; Rawson, 2009).

Hypothesis 2a – Activity budgets will adhere to the typical colobine pattern with a greater percentage of resting and feeding, followed by moving and socializing. More play activities will be observed among younger individuals.

Hypothesis 2b – There will be no significant differences between adult males and adult females given a probable lack of social hierarchy and the high degree of leaf eating.

Hypothesis 2c – Activity budgets will vary seasonally as they have in other studies on *Pygathrix* species (as noted above and detailed in Chapter 2).

1.2.3. Concerning feeding ecology

What plants are eaten? How flexible or diverse is the doucs' diet? What are the "keystone" and "fall-back" foods? In this study keystone foods, defined similar to van Schaik et al. (1993), are resources that produce edible materials throughout the year and are regularly exploited. Fall-back foods refer to foods that are only exploited when preferred foods are less abundant. To what degree does seasonality influence diet and food choice? To what degree do plant nutrients and chemicals influence food choice? Are the doucs selective feeders? In this study selective feeding refers to the selection of foods irrespective of their availability.

Rawson (2009) and Hoang Minh Duc (2007) showed that black-shanked doucs have relatively narrow dietary breadth with a low number of plant food species composing the diet, and only a few species accounting for a majority of the diet. Ha Thang Long (2009) alternatively reported a relatively wide dietary breadth with a high number plant food species. Additionally, studies of *Pygathrix* suggest that young leaves are preferred over older leaves, and fruits and seeds can comprise an equal or seasonally greater percentage of the diet than leaves (Hoang Minh Duc, 2007; Lippold, 1977; Lippold, 1998; Otto, 2005; Rawson, 2009). This challenges the understanding that *Pygathrix* diets are dominated by leaves (Davies & Oates, 1994; Kirkpatrick, 2011). In fact, numerous colobines rely heavily on seeds or fruits (Davies & Oates, 1994). Studies of colobines suggest that high protein low fiber foods are preferred (Davis and Oates, 1994; Oates, 1988b; Otto, 2005; Yeager et al., 1997), and that this protein-to-fiber ratio is a predictive factor in colobine biomass (Chapman & Chapman, 2002; Chapman et al., 2002; Fashing, 2007; Fashing, 2011; Oates et al., 1990). Content of tannins, phenolics, and fiber appear to have little effect on food choice (Fashing et al., 2007a; Kirkpatrick, 2011) as opposed to other primate species (Glander, 1981; Glander, 1982; McKey et al., 1981; Oates, 1977).

Hypothesis 3a– The doucs are highly selective feeders and their diet will be best characterized as a narrow dietary breadth with a few species accounting for the majority of their diet.

Hypothesis 3b – Fruit and flower selection will be significantly influenced by availability.

Hypothesis 3c – Forage quality influences dietary selection and protein enriched, low fiber foods will be preferred including young leaves over mature leaves.

Hypothesis 3d – Secondary compounds will not influence food selection.

Hypothesis 3e –Resource scarcity will involve mature leaves as fall-back foods.

1.3. Research significance

This study builds on previous studies of red-shanked doucs at Son Tra Nature Reserve, provides a basis for comparison with other long-term *Pygathrix* studies, and presents some of the first data on aspects of red-shanked douc socioecological (activity budget, habitat use, social structure, and feeding ecology). This study compares these data to broader colobine patterns, adding to current understandings and debates about primate evolution and adaptations.

This study highlights relationships between data and *in -situ* and *ex -situ* conservation activities (*i.e.*, diet in captivity, enhanced protection activities). Parts of this study explore threats to doucs and biodiversity of Son Tra and constructed maps and data (*i.e.*, ranging, feeding) are useful to Da Nang People’s Committee in addressing concerns of habitat fragmentation and protection. The fauna and flora of Son Tra are under serious risk of local extirpation, and this concern must be addressed properly if the doucs on Son Tra are to survive.

1.4. Dissertation outline

Chapter 2 includes a review of Colobinae phylogeny and *Pygathrix* ecology, focusing on the red-shanked doucs.

Chapter 3 describes Son Tra Nature Reserve, including our knowledge of the red-shanked doucs on Son Tra. Weather data and methodologies are presented. Methods used for phenology transects, behavioral observations, activity budget and feeding data are described.

Chapter 4 includes a description of forest types, plants communities and presents data on the phenology of leaf flushing, fruiting, and flowering.

Chapter 5 presents data on group size and composition, ranging behaviors, other observed social/group behaviors, and the influences of seasonality.

Chapter 6 presents data on the activity budget. This involves analyses of variation between sexes, ages and seasons.

Chapter 7 presents data on feeding ecology including food species, feeding times and patterns, nutritional and chemical quality, and how these relate to seasonality.

Chapter 8 concludes with a summary of the significant results and patterns, and how these data are having beneficial impacts for the conservation of the red-shanked doucs and Son Tra Nature Reserve.

Chapter 2. Review of *Pygathrix nemaeus*

2.1. Introduction

This chapter is divided into nine sections. The first section provides a review of phylogeny of colobines, and the second section reviews biogeography of Asian colobines. The third section reports on *Pygathrix* in more detail including physical description, locomotion, reproduction, and anatomy. The fourth section analyzes distribution and status of *P. nemaeus* in Vietnam. The fifth section reviews socioecology focusing on the influence of feeding ecology. The six, seventh, eighth, and ninth sections review diet, group composition, ranging, and activity patterns among colobines.

2.2. Phylogeny

2.2.1. Phylogeny of the Cercopithecidae

The family Cercopithecidae includes two subfamilies: Cercopithecinae (cheek-pouched monkeys) and Colobinae (leaf monkeys), also referred to as cercopithecines and colobines, respectively (Napier & Napier, 1967). The Colobinae likely emerged in Africa (Davies & Oates, 1994; Liedigk et al., 2012), spreading to Eurasia around 10 million years ago via a land bridge between Africa and the Arabian Peninsula (Stewart & Disotell, 1998). There continues to be debate concerning the date of the last common ancestor of the subfamilies, ranging from 13 to 19.5 mya (see Delson, 1994; Harrison, 1989; Liedigk et al., 2012; Meyer et al., 2011; Page et al., 1999; Roos et al., 2011; Sterner et al., 2006; Szalay & Delson, 1979). In this dissertation I generally follow the phylogenies presented by Liedigk et al. (2012) and Roos et al. (2011) for Asian colobine species. Figure 2.1 illustrates phylogenetic relationships.

The subfamilies are distinguished by several anatomical characteristics related to diet, locomotion, and encephalization. Colobines are predominately folivorous (Davies & Oates, 1994; Fashing, 2011; Kirkpatrick, 2011; Napier & Napier, 1967), and have a wide range of digestive and ingestive adaptations for processing fiber, seeds and secondary compounds in their diets that are lacking in cercopithecines (Chivers, 1994; Kay & Davies, 1994; Lucas & Teaford, 1994). Their diet accounts for mandibular differences between the subfamilies (Ravosa & Profant, 2000), the presence of higher cusped molars and lophids (Caton, 1991; Kay, 1977), less occlusal constriction and longer shear crest (Lucas & Teaford, 1994), and enlarged salivary glands (Groves, 1989; Waterman & Kool, 1994). Skeletal difference related to locomotion include a reduced or absence of an external pollex, and mid-tarsal shortening (Oates et al., 1994; Strasser & Delson, 1987). Using the Tenrecinae encephalization index there is no overlap between the two subfamilies with colobines ranging between 5.78 and 7.19 and cercopithecines ranging between 7.39 and 11.2 (Groves, 2000). All colobines with the exception of *Nasalis larvatus* have 44 chromosomes, whereas cercopithecines range between 42 and 72 (Groves, 2001a).

2.2.2. Phylogeny of the Colobinae

Colobines are divided into two tribes; Colobini (African colobines) and Presbytini (Asian colobines) (Figure 2.1). There is debate concerning the date of their last common ancestor, which ranges from nine to 15 mya (Delson, 1994; Liedigk et al., 2012; Meyer et al., 2011; Page et al., 1999; Roos et al., 2011; Sterner et al., 2006). Liedigk et al. (2012) placed this split between 11.84 and 12.25 mya, whereas Roos et al. (2011) placed this split at 10.9 mya.

Strasser & Delson (1987) noted that the Presbytini have a reduced external pollex, which is absent or rudimentary in the African colobines, and some contact between the lateral tarsals. Groves (1989) noted that the Asian colobines have shorter faces and suborbital fossa. Groves (2001a) recognized 59 species in total, including 15 species of three genera within the African colobines and 44 species of seven genera within the Asian colobines (Table 2.1). This dissertation follows the classification of Groves (2001a). For an alternative and reduced species list see Brandon-Jones et al. (2004).

Figure 2.1. Phylogeny of the Colobinae.
Based on dates in Liedigk et al. (2012), Roos et al. (2011), Ting et al. (2008) and Jinchuan Xing et al. (2005).

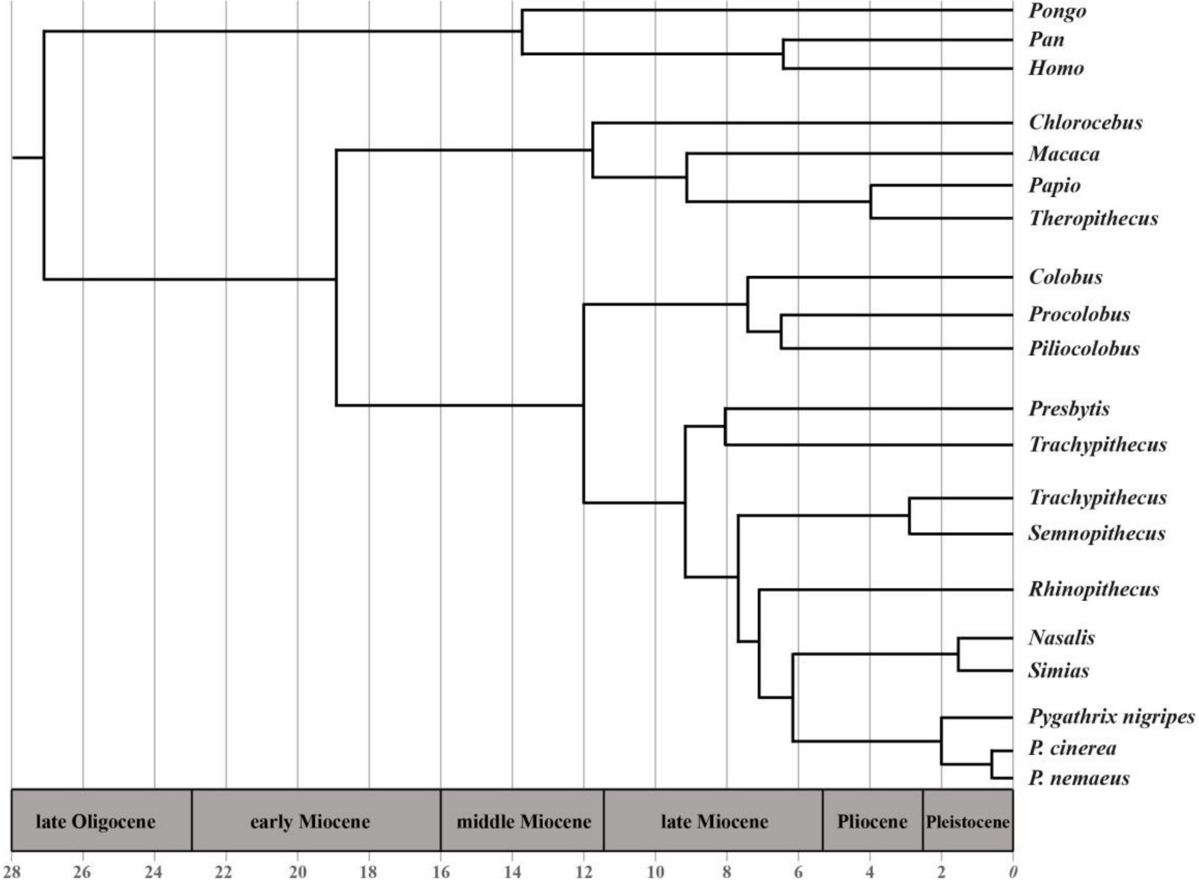


Table 2.1. Colobine genera and species numbers.
Based on Groves (2001a) and Geissman et al. (2011).

<table>
<tr><th colspan="8">Colobini – African colobines</th></tr>
<tr><td colspan="2">Genera</td><td colspan="2"><i>Colobus</i></td><td colspan="2"><i>Piliocolobus</i></td><td colspan="2"><i>Procolobus</i></td></tr>
<tr><td colspan="2">Number of species</td><td colspan="2">6</td><td colspan="2">8</td><td colspan="2">1</td></tr>
<tr><th colspan="8">Presbytini – Asian colobines</th></tr>
<tr><td></td><td colspan="3">Langurs</td><td colspan="4">Odd-nosed langurs</td></tr>
<tr><td>Genera</td><td><i>Presbytis</i></td><td><i>Semnopithecus</i></td><td><i>Trachypithecus</i></td><td><i>Nasalis</i></td><td><i>Pygathrix</i></td><td><i>Rhinopithecus</i></td><td><i>Simias</i></td></tr>
<tr><td>Species</td><td>11</td><td>7</td><td>17</td><td>1</td><td>3</td><td>5</td><td>1</td></tr>
</table>

2.2.3. Phylogeny of the Presbytini

Asian colobines are further divided into two groups; langurs and odd-nosed monkeys. Divergence date estimations range from five to 10 mya (Delson, 1994; Liedigk et al., 2012; Meyer et al., 2011; Page et al., 1999; Roos et al., 2011; Sterner et al., 2006). Liedigk et al. (2012) and Roos et al. (2011) reported similar divergence dates between 7.7 and 8.9 mya.

Odd-nosed colobines share modifications to the nose. The nasal bones are either reduced (*Pygathrix, Rhinopithecus*) or lengthened (*Nasalis, Simias*) (Groves, 2001), a developmental synapomorphy that Jablonski (1998) identified as distinguishing odd-nosed colobines from other Asian langurs. Groves (2001a) reported higher intermembral indices among odd-nosed colobines. Jablonski (1998) noted limbs are nearly of equal lengths, and odd-nosed colobine infant pelage is not as exceptionally distinct in color relative to the adult pelage as it is in langurs, with the exception of infants of the *Simias*.

2.2.4. Phylogeny of the odd-nosed colobines

There remains debate concerning which odd-nosed colobines are more derived and which retain the more ancestral characteristics, with nearly every genus having been suggested to be either more derived or more ancestral, and nearly every genus having been suggested to be most closely related to one another (Bigoni et al., 2003; Bigoni et al., 2004; Caton, 1998; Groves, 2000; Jablonski, 1998; Jablonski & Yan-Zhang Peng, 1993; Karanth et al., 2008; Kirkpatrick, 1995; Liedigk et al., 2012; Meyer et al., 2011; Oates et al., 1994; Page et al., 1999; Pan & Oxnard; 2001, Roos, 2003; Roos, 2004; Roos et al., 2007; Roos et al., 2011; Pan et al., 2004; Sterner et al., 2006; Ting et al., 2008; Wen Wang et al., 1997; Xiao Ping Wang et al., 2012; Zhang Yaping & Ryder, 1998a; Zhang Yaping & Ryder, 1998b; Yan-Zhang Peng et al., 1993).

Roos et al. (2011) and Liedigk et al. (2012) suggested a basal split between *Rhinopithecus* and the other odd-nosed colobines between 6.43 and 7.28 mya. This was followed by a split between *Pygathrix* and the *Nasalis-Simias* clade between 5.66 and 6.63 mya, and a split between *Nasalis* and *Simias* between 1.06 and 1.92 mya. In light of the relatively recent split between *Nasalis* and *Simias*, Liedigk et al. (2012) suggested autopomorphic traits may only need a short time to emerge.

2.2.5. Phylogeny and classification of *Pygathrix*

Houck et al. (2010), Roos (2004), Roos & Nadler (2001), and Roos et al. (2007) genetic analyses supported the classification of three *Pygathrix* species, and indicate *P. nigripes* diverged first, followed by a split between *P. nemaeus* and *P. cinerea*.

Recognition of *P. nigripes* as a distinct species began with the description by Milne-Edwards (1871) of *Semnopithecus nigripes* from Ho Chi Minh City. Following this, a description of *Presbytis nemaeus moi* (Kloss, 1926) from Lang Bian, Vietnam was initially thought to represent a subspecies of *P. nigripes* based on reduced black coloration. However, numerous studies have shown that *P. moi* is synonymous with *P. nigripes* (Roos, 2004; Roos & Nadler, 2001; and Roos et al., 2007)

Recognition of *P. cinerea* as a species began with Wirth et al. (1991) who described a douc in the wildlife markets of Ho Chi Minh City with distinct coloration. Nadler (1997) classified this individual from the market as a subspecies of the red-shanked douc, naming it *Pygathrix nemaeus cinereus*. The latter part of the name was quickly changed to *cinerea* to account for the feminine suffix (Timmins & Duckworth, 1999). Based on genetic and morphological studies it was recognized as a distinct species, *P. cinerea* (Groves, 2001a; Roos & Nadler, 2001). These relationships are illustrated in Figure 2.2.

Count de Buffon’s *Histoire Naturelle* (Buffon, 1766) provided the first scientific report on the red-shanked doucs. Figure 2.3 shows one of his penciled sketches of a red-shanked douc, reprinted with due provenance. Buffon first named these primates Doucs and described their long tail, flattened nose, equal limb lengths, reduced pollex, distinct beard, and reddish-brown with yellowish facial and ear tones. Buffon’s descriptions are based on a single stuffed individual, and Buffon noted the possibility of dehydration which results in hair and skin fading (see Groves, 2007a for a photo of this specimen). Carl von Linné’s 6th edition of *Mantissa Plantarum* (Linnaeus, 1771) included the first scientific classification of the doucs within the primate order; *Simia nemaeus*. Linné retained the common name Douc. Étienne Geoffroy St. Hilaire (1812) placed the doucs into a new genus; *Pygathrix*. His classification of *Pygathrix nemaeus* has been maintained. “Pyga” in Latin translates to rump or buttock; “thrix” in Latin is derived from the Late Greek work *thrix* which means hair; *nemaeus* is based on the Latin *nemas* meaning forest or grove. *Pygathrix* therefore pays homage to Buffon (1766) who argued that the presence of hair on the buttock of doucs in conjunction with other characteristics placed them phylogenetically between monkeys and apes.

Figure 2.2. Phylogeny of *Pygathrix*.
Adapted from Roos (2004). Haplogroups of *P. cinerea* are included.

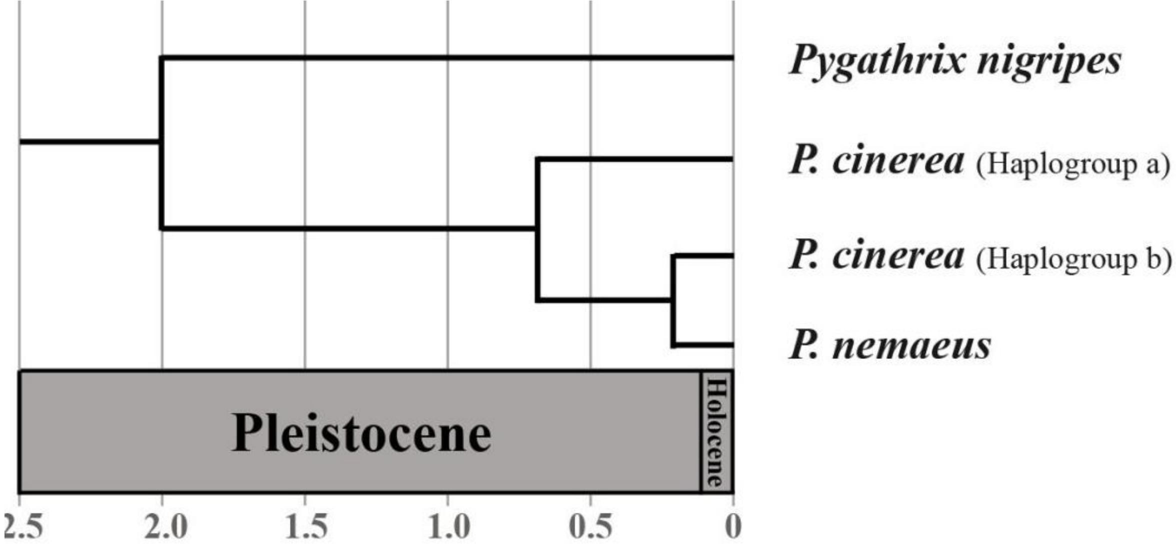


Figure 2.3. Buffon's (1766: 302) penciled sketch of a red-shanked douc.
Reprinted with permission from the Directors of Publication of Buffon et l'histoire naturelle: l'edition en ligne, Dr. Pietro Corsi of the University of Oxford and Dr. Thierry Hoquet of the l'Université de Paris, copyright www.buffon.cnrs.fr, 2013.

2.3. Biogeography

Davies & Oates (1994) and Liedigk et al. (2012) reported the subfamily Colobinae emerged in Africa, and Stewart & Disotell (1998) suggested they spread to Eurasia about 10 mya. Delson (1994) revealed that the Eurasian colobine fossil record suggests slow species diversification peaking with extant taxa, whereas the African colobine fossil record suggests rapid speciation into the Pliocene followed by extinction to extant taxa. In the late Miocene and

Pliocene in certain geographic areas such as southern Europe and East Africa, colobines appear to have been more diverse and abundant than cercopithecines (Fleagle, 2013).

The Hengduan Mountains of Burma, China and India were a core area and diversification zone for ancestral colobines (Jablonski, 1998; Liedigk et al., 2012; Roos et al., 2011; Van Ngoc Thinh et al., 2010). The Mekong, Salween, and Yangtze rivers all arise in these mountains. Hallet & Molnar (2001) noted that for nearly 300 km these rivers are only a few km apart and nowhere else in the world are rivers of these lengths so close together. Meijaard & Groves (2006) suggested that these rivers have been barriers to biota since the early Miocene.

Jablonski (1998) argued the ancestor of a possible *Nasalis-Pygathrix-Mesopithecus-*R*hinopithecus* clade occupied a core area around the Hengduan Mountains characterized by broadleaf deciduous and evergreen forests. As the primates began to spread south, cycles of landscape dissection from river flow and tectonic uplift resulted in allopatric speciation (Liedigk et al., 2012). Fooden (1996) and Groves (2007a) highlighted that the Mekong River is a significant barrier, and several genera and species of primates are found only on the east side including *Pygathrix*, *Nomascus*, *Rhinopithecus*, the limestone langurs (certain species of *Trachypithecus* adapted to limestone habitat) and *Nycticebus pygmaeus*. This barrier does not predict vicariance. Meijaard & Groves (2006) and Groves (2007a) reported that *Trachypithecus germaini*, *T. phayrei*, *Nycticebus bengalensis* and various macaques are found on both sides of the river. An Zhisheg et al. (2001) noted tectonic uplift affected the weather and temperature patterns over much of Asia which intensified summer and winter monsoons. Dengke Hu et al. (2012) and Zhifei Liu et al. (2003) reported glacial and interglacial fluctuations further affected monsoonal patterns by intensifying the summer and weakening the winter monsoons during interglacial periods, with the inverse pattern occurring during glacial periods. These patterns have been highly variable over the last seven million years (Dengke Hu et al., 2012; Hongbo Zheng et al., 2004; Zhifei Liu et al., 2003; Zhongli Dinh et al., 2001). Zhengtang Guo et al. (2004) noted the uplift of the Tibetan Plateau and recurring glaciation events are prominent forces in the desertification of central China and the aridification of eastern Asia during late Miocene and Pliocene times. Meijaard & Groves (2006) and Groves (2007a) argued that these patterns led to the creation of refuge areas as the tropical zone migrated south with the advance of the subtropical and temperate zones.

Odd-nosed monkeys in the late Miocene migrated south into Indochina and the Sundaland Islands via land bridges (Jablonski, 1998; Liedigk et al., 2012; Roos et al., 2011). The Sunda shelf and low sea levels 18 kya allowed for a forested connection between the mainland and islands (Sterling et al., 2006). Species of *Pygathrix* and *Rhinopithecus* differentiated during the late Pleistocene, and *P. nemaeus* and *P. cinerea* diverged during the mid-Pleistocene. Liedigk et al. (2012) suggested that speciation within *Pygathrix* resulted from changes in climate and habitat in the Annamite Mountains.

In Vietnam there are northern temperate climates and southern tropical climates (Sterling et al., 2006). Groves (2007a) illustrated primates either replace each other via vicariance or are restricted to one region. For example, *Macaca assamensis* and *M. leonine*, and *Trachypithecus crepusculus* and *T. germaini* / *T. margarita* replace each other with no range overlap, *Macaca mulatta* and *M. fascicularis* overlap and hybridize, and *Pygathrix* species have minimal overlapping zones. Fooden (1996) noted a north-south taxonomic disjunction between 14 and 17 degrees north among rodents, birds, fish and primates. Only a few primate species (including *Macaca arctoides* and *N. bengalensis*) are not limited by this north-south divide.

The Annamite Mountains with their remnant populations of doucs, such as those on Son Tra Nature Reserve, represent refuge areas for numerous endangered and endemic animals and plants now on the brink of extinction due to anthropogenic factors.

2.4. Descriptions and characteristics

2.4.1. Descriptions of *Pygathrix*

Pygathrix species have been described as among the most colorful primates in the world (Hoang Minh Duc, 2007; Jablonski, 1998; Lippold, 1977; Nadler et al., 2003; Oates et al., 1994). Doucs have a long tail nearly equal to their head-body length, and their nose is flat with flaps of skin partially covering the nares (Nadler et al., 2003). It is often reported that there is little to no sexual dimorphism in body size or coloration (Fleagle, 2013; Napier, 1985; Oates et al., 1994). This is inaccurate. During this study identifying adult males from adult females was relatively easy based on body size dimorphism. Similar ease in identifying males from females has been noted by other *Pygathrix* researchers (Herbert Covert, personal communication. 2013). This differentiation is not as pronounced as reported among some colobines (see Oates et al., 1994), but there is sexual dimorphism of body size.

Pygathrix species are distributed along the Annamite Mountains. In Vietnam, *P. nemaeus* (red-shanked douc) is located in north-central and central Vietnam, *P. cinerea* (grey-shanked douc) is in central and south-central Vietnam, and *P. nigripes* (black-shanked douc) is in south central and southern Vietnam (see Figure 2.4). Phenotypic differences between these species include the color of their lower legs, facial skin tones, and axis of the eyes. Red-shanked doucs have red hair on their legs, yellowish to light brownish toned facial skin and a high axis of the eyes (20.9°), grey-shanked doucs have grey hair on their legs, similar facial tones to red-shanked doucs but a lower axis of the eyes (14.6°), and black-shanked doucs have black hair on their legs, light bluish toned facial skin, and an eye axis at 11.2° (Lippold & Vu Ngoc Thanh, 1995; Nadler et al, 2003). Table 2.2 presents a detailed physical description of the three species and Table 2.3 presents information on head-body length, tail length and weight. Figure 2.5 illustrates the three douc species.

Infants of all three species have a similar appearance. Infant coloration of most odd-nosed colobines is more similar to adult pelage than in langur species, but there are infant-adult pelage differences. Infants of *Pygathrix* have darker more bluish faces with yellow rings around the eyes similar to adult *P. nigripes* (Nadler et al., 2003). This changes to the adult coloration around 2 years of age (Nadler et al., 2003), and males do not grow the adult whiskers (another possible sexual dimorphic characteristic) until around 4 years of age (Ruempler, 1998). Table 2.4 presents basic developmental stages.

There are color variations within species. Some populations of red-shanked doucs have a decrease in the red color and degree of red hair on the legs (Coudrat et al., 2012). Around Phou Ahyon in Laos the red hair on the lower legs is reduced to small patches and is dull, and farther south near Nam Ghong the red hair is only in small bands around the ankles, with the remaining leg hair being blackish (Coudrat et al., 2012). On Son Tra Nature Reserve I have observed a red-shanked douc of similar description. Black-shanked doucs in Hon Heo of Khanh Hoa Province exhibit color variation on the forearms (white hair ranging from wrist bands to entirely white forearm) and on the lower legs (red hair on the lower half of the lower leg), both of which are features typical for red-shanked doucs (Nadler, 2008). Nadler et al. (2003) noted possible hybrids between red-shanked and grey-shanked or grey-shanked and black-shanked doucs based on intermediate coloration in specimens described in various reports. Lippold et al. (2011) describes color variations in a population of red-shanked doucs in Mom Ray National Park, Vietnam, which may result from hybridization with either grey-shanked or black-shanked doucs. Rawson & Roos (2008) and Rawson (2009) suggested that hybrids also exist in Cambodia, providing evidence of possible mixed genetic content along with observations of color variation.

Figure 2.4. Distribution map of species of *Pygathrix*.

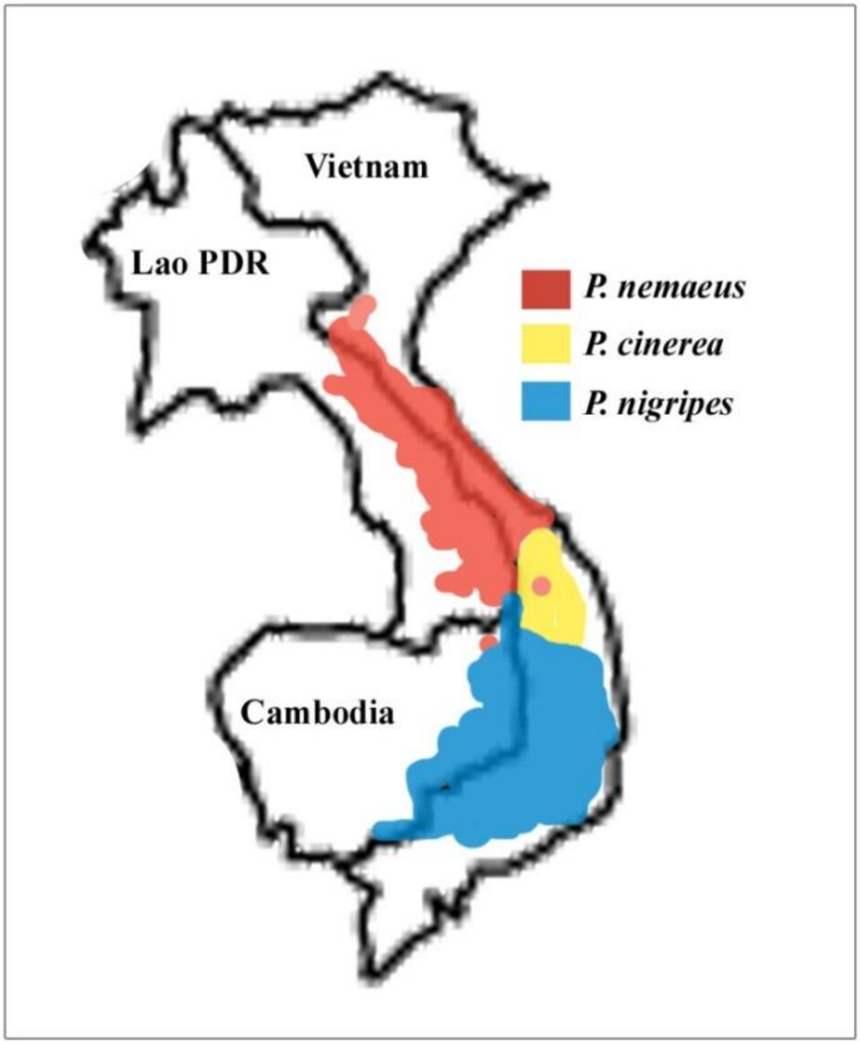


Figure 2.5. Photos of the three species of *Pygathrix*.

P. nigripes (left) credited to Hoang Minh Duc, *P. nemaeus* (center) credited to Larry R. Ulibarri, and *P. cinerea* (right) credited to Ha Thang Long.

Table 2.2. Physical descriptions of *Pygathrix*.

Adapted from Chaplin & Jablonski (1998), Lippold (1977), Nadler (1997) and Nadler et al. (2003).

P. nemaeus
• Head: Agouti hair on crown and temples. Crown hair is silver grey. Temple hair is red or chestnut. Hairs of forehead are black. Ear tufts are red or chestnut. Whiskers are white or bleached and measure up to 12 cm in adult males. Hairs of cheeks are white or bleached. • Body (Ventral): Hairs of throat are white or bleached. Hairs of the collar are orange with a black band from shoulder to shoulder. Hairs of inner arms are black. Hairs of inner thighs are black and agouti. Hairs of the lower legs are red or chestnut. Ventral coat is silver and agouti. • Body (Dorsal): Hairs of nape of neck are agouti. Hairs of deltoid area are black. Hairs of lateral sides of arms are agouti. Hairs of forearms are white or bleached. Hairs of the triceps area are silver grey and agouti. Hairs of back of hands are black. Hairs of the back are silver grey and agouti. Hairs of the sacral area are white or bleached. Hairs of the iliac area are black. Hairs around the perineum area are white or bleached. Hairs of the back thigh are black. Hairs of the lateral thighs are black. Hairs of the lower legs are red or chestnut. Hairs of the feet are black. Hairs on the tail and tail tip are white or bleached. • Skin: Facial skin is considered to have a yellowish to light brownish tint. Skin around the eyes is this flesh coloration, on the eyelids it is more bluish colored. Nasal skin is flesh colored. Philtrum skin is flesh colored. Supralabial skin is red. Actual lip skin is red. Ear skin is flesh colored. Palm of hand skin is black. Foot skin is black. Nipple skin is black. Ischial callosities skin is flesh colored. Perineal and surrounding skin is red. Penis skin is red. Scrotum skin is white. • Hypertrichy: Tail hair length is short. Withers hair length is considered normal. Sacrum hair length is short. Cape hair length is short. Sexual dimorphism of coat is absent. Navel tuft or whirl is present. Ventral line hypertrichy absent. Vertex cresting absent. Head crown swirl or whorls absent. Ear tufts present. Whiskers present with swept back whiskers also present. Tail length to body shortened. Monocolored tail. Tail tuft present. Side of tail hypertrichy absent. • Nasal morphology: Lateral crus of the greater alar cartilage is slightly expanded into the minor ros tral extension. Lacks ridge on nasal skin.

P. cinerea
Same as the red-shanked doucs except: • Head: Whiskers tend to be shorter and sparser compared to red-shanked doucs. Hairs of the forehead are also black but the band is smaller compared to red-shanked doucs. • Body (Ventral): Hairs of inner arms are silver. Hairs of inner thighs are silver. Hairs of the lower legs are silver. Ventral coat is generally lighter silver than in red-shanked doucs. • Body (Dorsal): Hairs of deltoid area are silver. Hairs of lateral sides of arms are silver. Hairs of forearms are silver. Hairs of the back are significantly longer than in the other *Pygathrix* species (Stefen & Szokoli, 2010). Hairs of the iliac area are silver. Hairs around the perineum area are white or bleached. Hairs of the back and lateral thighs, and lower legs, are silver.
P. nigripes
Same as red-shanked douc except: • Head: Ear tuft is white or bleached. Whiskers are yellow. Whiskers tend to be shorter and thinner compared to red-shanked doucs. Hairs of the cheeks are yellow. Hairs of forehead are black and run in a band along the sides of the head down to the shoulders. • Body (Ventral): Hairs of throat are yellow. Hairs of inner arms are black with a reddish hint. Hairs of upper arms are black. Inner thigh hair is grey. Hairs of lower legs are black. • Body (Dorsal): Hairs of forearm are black. Hairs of lower legs are black. Hairs of the sacral area are also white or bleached but the patch is smaller compared to red-shanked and grey-shanked doucs. • Skin: Facial skin is bluish in tint except around the eyes, which is yellowish to light brownish. Penis skin is light red. Scrotum skin light blue.

Table 2.3. Body measurements of specimens of *Pygathrix* species.

Adapted from Nadler et al. (2003), Kirkpatrick (1998), and personal communications with Tilo Nadler (2013).

		Head-Body Length (mm)	Tail Length (mm)	Weight (kg)
P. nemaeus	Male	550 - 820	560 - 735	8.6 – 11.4
	Female	597- 630	440 - 597	6.6 – 10.5
P. cinerea	Male	620 - 640	640 - 650	10.7 - 12.4
	Female	560 - 580	590 - 640	7.5 - 9.4
P. nigripes	Male	590-698	670-769	11.1
	Female	550-585	560-735	6.0

Table 2.4. Developmental stages of *P. nemaeus*.
Adapted from Lippold (1977) and Ruempler (1998)

Developmental stage	Age range	Description
Newborn / Infant	0 to ~8 months	Face is blackish blue, pale yellowish stripes under eyes. Hair on the head is dark with chestnut band along forehead. Body hair is pale chestnut-colored wide black patch extending from shoulders to the rump. Hair of arms, legs and rump are darker chestnut color. Hands and feet are black; tail is reddish grey. Behaviorally, not weaned, remain with or near mother frequently, locomotor skills poor, suckling but increasing consumption of solid foods.
Infant	8 to ~18 months	Adult coat coloration begins to appear. Face remains blackish blue but gradually changes coloration to adult pattern. Adult pattern of coloration of body begins including white hairs on cuffs and tail, maroon hair on legs, grey body hairs, and among males white hair in a circular patch on rump might start to form. Testicles descend, scrotum more visible, penis becomes reddish pink. Behaviorally, not weaned but spend more time away from mother at further distances, play behavior is frequent, consumption of solid foods frequent although suckling still continues. Weaning might begin around 12 months.
Juvenile	~18 months to ~3 years	Adult coat and facial integument is developing although there may still be blackish blue facial skin around the eyes and cheeks (changing first) and around the nose, mouth and chin (changing last). Body size is larger than infant but considerably smaller than adults. In males the long facial whiskers remain undeveloped. Behaviorally they are usually weaned, spend more time away from mothers and at greater distances than infants, play frequently, and beginning to participate in other social behaviors often such as grooming, auto-grooming and threat displays.
Subadult	~2.5-3.5 years in females and ~3-4 years in males	Adult coat and face are developed although may be paler compared to adults. Adult body size is nearly achieved, but individuals may be visibly smaller than adults. Males have not developed the long whiskers on the face especially the chin. Behaviorally subadults are similar to adults, although submissive behaviors are usually more frequent.
Adult		Sexually and physically mature.

2.4.2. Reproduction, development, and care

For red-shanked doucs at Cologne Zoo, Ruempler (1998) reported females and males first exhibit sexual behaviors at three years of age, and females give birth between five and eight years. Kulcharoen & Utara (2010) reported that at Dusit Zoo sexual behavior begins at three years of age, but females first gave birth at just over four years of age, and fathering males were between four and five years of age. Lippold (1989) observed that females from San Diego Zoo first gave birth at 4.5 years of age, and fathering males were 5.5 years of age. Ruempler (1998) noted the oldest recorded birthing was by a 26 year old female. Females indicate sexual receptiveness through crouching behavior, observed in both red-shanked (Lippold, 1977; Ruempler, 1998), and black-shanked doucs (Nadler, 2008).

Ruempler observed estrus occurs every 28 to 30 days and is accompanied by reddening of the skin on the rump (another diamorphic trait). Lippold (1977) noted this reddening occurs on the inguinal area and persists during pregnancy. Heistermann et al. (2004) reported that females in Cologne Zoo have an ovarian cycle of 26.5 days, based on fecal samples. Brockman & Lippold (1975) estimated gestation length at 180-200 days from San Diego Zoo based on observations of copulation and births. However, copulation occurred regularly during pregnancy, and Ruempler (1998) highlighted this weakness in their estimate. Lippold (1977) added an estimated gestation length of 165 days based on her personal communication with Ute Hick, an animal keeper at Cologne Zoo. Lippold (1981) reported gestation length was 210 days based on urine analyses. Ruempler (1998) noted that estrus begins again nine months after birthing, and the interbirth interval averaged 24 months (16 to 38 months). Kulcharoen & Utara (2010) reported an interbirth interval of 16 months (9 to 26 months).

Lippold (1977) reported birth peaks in March and October but noted that births occurred throughout the year. Ruempler (1998) reported birthing peaks around February and September, and also noted that births occurred throughout the year. Kulcharoen & Utara (2010) observed birthing peaks in March/April and September, also noting that births occurred throughout the year. Phiapalath (2009) and Phiapalath et al. (2011) reported observing 15 wild births suggesting a birthing season entirely within the rainy season (from May to October), and a mating season which peaks between November and January (early to middle dry season).

Ruempler (1998) noted that birthing is done while sitting in the upper portions of the enclosures (as opposed to on the ground), usually occurred between 19:00 and 20:00, and the infants immediately grasped the female’s chest with hands and feet. At five days old infants began to interact with other group members and by days six and seven infants played. During day 18 food-sharing behaviors were observed. At four weeks old, infants began to move farther from the mother, and to clutch onto the father regularly (Schwierz, 2013). At 60 days deciduous teeth erupted and they ingested fruit and leaves. Bett (2011) reported on grey-shanked doucs in captivity, also noting that at about two months of age infants began to move away from their mothers. Yeong et al. (2010) observed infant red-shanked doucs from Singapore Zoo ingested solid foods during the second month, and increased independent travel between 60 and 90 days. Weaning typically starts between 12 and 15 months, but suckling has been witnessed to continue in individuals two years of age (Bett, 2011; Ruempler, 1998). Yeong et al. (2010) reported that weaning begins as early as five months, but during their study period only one infant was observed to be fully weaned at 16 months, and all other infants were still in the process of being weaned. Lippold (1995) indicated that weaning begins at 12 to 13 months.

Ruempler (1998) reported that aggression is extremely rare in captivity, mostly involving male juveniles and subadults being chased by adult males. Aggression also involved threat displays consisting of flattening the ears, stretching the neck outwards, staring and vocalizing. Juveniles typically responded with submissive behaviors including repetitive gestures, screams, and placing their head on the abdomen of the adult male. Infants are always protected, tolerated, never displaced while feeding, and adult males and females were tolerant of play behavior including being jumped on and their tails used for swinging.

2.4.3. Locomotion

Captive red-shanked doucs at the Endangered Primate Rescue Center, Vietnam, have been the focus of several locomotor studies (Byron & Covert, 2004; Covert et al., 2004; Stevens et al., 2008; Workman & Covert, 2005). Prior to these studies, colobines in general including doucs were presumed to be arboreal quadrupeds, although Napier & Napier (1967) classified them as semibrachiators. The use of jumping or dropping from upper to lower canopy levels has been noted by these and several other researchers. Byron & Covert (2004) and Covert et al. (2004) showed that individuals of species of *Pygathrix* use brachiating behaviors frequently. Covert et al. (2004) reported this behavior is reflected in their skeletal anatomy; certain anatomical measures diverge from other Old World monkeys towards the anatomy of suspensory hominoids.

2.4.4. Dental morphology

Dental morphology of colobines permits for efficient processing of fibrous material. Their teeth are characterized by high crowned molars with high cusps and long shear crests, short molar trigonids, and narrow incisors (Kay, 1978; Lucas and Teaford, 1994). Hylander (1975) and Kay & Hiiemae (1974) reported that more frugivorous taxa have larger anterior teeth for processing fruit and more folivorous taxa have larger molars for grinding and shearing leaves. The second incisors of colobines are often the same size or larger than their first incisors, and molars are not always larger than those of macaques (Pan, 2007; Wright & Willis, 2012). Pan & Oxnard (2003) and Pan (2007) found that within Asian colobines, individuals of species of *Rhinopithecus* and *Semnopithecus* have larger molars per body size than do individuals of species of *Pygathrix*, *Nasalis*, *Trachypithecus* and *Presbytis*, and even compared to the Asian macaques, although different methods for molar size were used (length, width and height in the former, and length and width in the latter). Reasons for this might be related to dietary adaptations, and Pan & Oxnard (2001) suggested that individuals of species of *Rhinopithecus* and *Semnopithecus* exploit unique vegetation in temperate environments near the Tibetan Plateau and Qingling Mountains. In contrast, individuals of species of *Pygathrix*, *Nasalis*, *Trachypithecus* and *Presbytis* eat more leaves and fruits, and are distributed in tropical environments. Pan (2006) reported that Asian colobines tend to have larger canines than African colobines. Some features of the mandible such as the condylar, mandibular corpus, and mandibular symphysis areas indicate that individuals of species of *Rhinopithecus* are more robust than in other colobines (Jablonski et al., 1998). These features suggest that individuals of *Rhinopithecus* species (notably *R. brelichi* and *R. avunculus*) process mechanically tougher foods (Jablonski et al., 1998; Le Khac Quyet et al., 2007). Individuals of species of *Pygathrix* also have a shallower and more gracile mandibular corpus than do individuals of species of *Trachypithecus*, which tend to have longer chewing rates and larger molars, highlighting the digestive over ingestive emphasis of *Pygathrix* (Wright et al., 2008a).

2.4.5. Digestive anatomy

2.4.5.1. Colobines

Digestive adaptations of colobines have long been a focus of study (Caton, 1998; Duvernoy, 1834; Otto, 1835; Pilliet & Boulart, 1898). Colobines have an expanded and segmented forestomach (Chivers, 1994; Chivers & Hladik, 1980) which supports microorganisms and allows for fermentation of structural polysaccharides (Caton, 1998; Chivers, 1994; Kay & Davies, 1994). This compartment is a unique adaptation among primates. Colobines also have a relatively large caecum and proximal part of the colon (Chivers, 1995; Kay & Davies, 1994) which are sites of additional bacterial fermentation (Caton, 1990).

In the rumen there are a number of microbes (bacteria, protozoa and fungi) that aid in cellulose and hemicellulose plant digestion (Kay & Davies, 1994). Microbes in the saccus gastricus produce B vitamins that are useful to the host animal, and volatile fatty acids (principally acetic, propionic and butyric acids) that acidify stomach contents (Kay & Davies, 1994). The volatile fatty acids and bacterial cells can be converted to microbial protein, which is a valuable supplement in a low protein diet. Digesta passes through the system slowly as a result of fiber content, allowing for the conversion of cellulose to volatile fatty acids and other byproducts (Kay & Davies, 1994). Ingesta are separated between the proximal saccus gastricus and acidic distal tubus gastricus and par pylorica (Bauchop, 1978). The proximal section of colobine stomachs has a pH value between 5.0 and 8.0 (Kay & Davies, 1994; Sunderland-Smith et al., 1998). The lower pH values were associated with low fiber diets in captivity. Sunderland-Smith et al. (1998) reported that lower pH values were found among unhealthy animals, whereas healthy animals had pH values between 6.5 and 8.0. The maintenance of pH balance is important in supporting a large and diverse microbacterial flora (Kay & Davies, 1994). The distal regions are characterized by lower pH values (~2.4) indicating acidic digestion (Kay et al., 1976). If the diet is lacking in fiber the digesta passes through the gastrointestinal tract too quickly, the microbacteria die, and the pH levels drop (Milton, 1984a). Also, if the diet is overly enriched in fiber the production of volatile fatty acids during fermentation exceeds the absorption of these acids, which also results in decreased pH levels and a condition called acidosis that can be fatal (Lambert, 1998; Nijboer & Clauss, 2006). Colobines need to maintain fiber intake balance in order to maintain a pH balance and a healthy digestive physiology.

Bauchop (1978) reported after ingesta leaves the stomach, fermentation products can be absorbed at small intestine functional sites. Kay et al. (1976) reported high volatile fatty acid concentrations in the caeco-colon comparable to those in the proximal stomach, indicating that fermentation occurs at both sites. Nijboer et al. (2006) reported long particle retention times among colobines, with most being over 40 hours.

Bacteria can synthesize vitamins, and increase the vitamin content of ingesta, making an animal virtually independent of dietary sources of all vitamins except A and D (Bauchop, 1978). The contribution of microbial protein and vitamins to overall protein and vitamin balance in leaf eating monkeys has yet to be studied and quantified. This illustrates the need for caution when measuring only dietary protein or vitamins (Yeager et al., 1997).

Microbacteria and fermentation reduce the harmful effects of toxic compounds, and colobines have higher fiber and secondary compound tolerances than nonspecialized folivores (Janzen, 1978; Garber, 1987). Secondary plant compounds such as tannins reduce digestibility and are often toxic, and therefore they should influence food choice. However, phenolic secondary compounds are not avoided by colobines (Burgess and Chapman, 2005; Davies & Bennett, 1988; Hoang Minh Duc et al., 2009; Kool, 1992; McKey et al., 1981; Mowry et al., 1996; Oates et al., 1980; Workman, 2010). According to Clauss (2003) the large salivary glands of colobines produce tannin binding proteins similar to those of ruminants. The negative effects of tannins may also be reduced through geophagy (Müller, 1996; Oates, 1978; Rawson, 2009). Complex gut adaptations allow colobines to exploit food resources that cannot be beneficially exploited by other primates (Fashing, 2001a). This dietary specialization may have evolved to allow colobines to feed on leaves which are abundant but otherwise indigestible (Andrews & Aiello, 1984). Others have suggested that this adaptation relates to indigestible compounds and toxins in fall-back foods (Chivers, 1994, Lambert, 1998; Fashing, 2001a).

As noted by Lambert (1998), gastrointestinal form alone cannot predict diet. In relating diet to morphology (gastrointestinal and dental), morphology only reveals the broad limits of what diet can be, not what it is (Milton, 1984a; Janson & Boinski, 1992). Feeding ecology studies on colobines show that these primates are not necessarily or preferably folivorous despite adaptations to folivory.

2.4.5.2. Distinctions in the gut morphology of species of *Pygathrix*

Individuals of species of *Pygathrix* are distinct from other Asian colobines in having a stratified squamous epithelium lining on the presaccus and cardiac glands, and the stratified cardiac glands extend into the submucosa of the saccus gastricus (Canton, 1998). Although the presaccus of individuals of *Nasalis* are similarly lined, no other colobines studied to date have stratified cardiac glands and none have the extension of these glands into the submucosa. Canton (1998) speculated the presaccus can act as a “gastric mill”, reducing the size of ingesta before entering the saccus as among avian species.

2.5. Distribution, population, and status

2.5.1. Distribution

Pygathrix nemaeus is found in central Vietnam from 19°22’N to 14°22’N (Ha Thang Long, 2007; Ha Thang Long, 2009; Lippold, 1977; Nadler et al., 2003; Pham Nhat, 1993a; Pham Nhat, 1993b). In Laos they are found from 18°38’N to the Cambodian border at 14°25’N (Timmins & Duckworth, 1999). Rawson & Roos (2008) reported sightings of *P. nemaeus* (or possible hybrids between *P. nemaeus* and *P. cinerea*) in Cambodia near the Laos border at 14°01’N (a southward extension of their distribution by 50 km).

In Vietnam, records for *P. nemaeus* based on sightings, interviews, specimen collections, and confiscations come from 17 sites. Of these sites, six have confirmation of red-shanked doucs in the last six years, five have confirmed or suggested red-shanked doucs in the last 25 years, and six are based on interviews, specimen collections, and confiscations. This information is reviewed from north to south with notes about site characteristics, and Table 2.5 summarizes the data with reference to the site locations shown in Figure 2.6.

Site 1– Pu Mat National Park in Nghe An Province is 91,113 ha, predominately covered by lowland evergreen forests with areas of lower montane evergreen forests, and elevation ranges up to 1,841 m (Birdlife International Sourcebook, 2004). It is located along the northern Annamite range, and borders Laos. Lippold (1998) reported sightings of groups of 25 to 35 individuals during surveys between 1993 and 1996, but no sighting of the doucs have been reported since (Nadler et al., 2003). Heavy logging combined with hunting and mining activities are noted as threats (Birdlife International Sourcebook, 2004).

Site 2– Vu Quang National Park in Ha Tinh Province is 55,029 ha which was logged and heavily exploited until 1993. It is predominately covered by lowland evergreen forests with areas of lower montane evergreen forests and the elevation ranges between 30 to 2,286 m (Birdlife International Sourcebook, 2004). It is part of the northern Annamite range bordering Laos. In 2000, Pham Nhat reported a sighting of one group of unrecorded size, and hunting was noted as a major threat (Nadler et al., 2003).

Site 3– Ke Go Nature Reserve in Ha Tinh Province is 24,801 ha which was entirely under the management of logging companies until recently. The forest is noted as heavy disturbed lowland evergreen and elevations range from 50 to 497 m (Birdlife International Sourcebook, 2004). No sightings have been reported and presence is based on specimen and interview data (Nadler et al., 2003).

Site 4– Huong Son District in Ha Tinh Province. In 1985, four to seven douc individuals were seen in this district, and doucs were again reported in 2000 (Nadler et al., 2003).

Site 5– Phong Nha-Ke Bang National Park in Quang Binh Province is 85,754 ha. The forest is largely undisturbed and mostly lowland evergreen, and it contains one of the largest remaining areas of limestone karst with elevations up to 400 m (Birdlife International Sourcebook, 2004). Haus et al. (2009) suggested that the population of red-shanked doucs is between 445 and 2,137 individuals. The latter end of their estimation is high, and Coudrat et al. (2012), Haus et al. (2009), and Nadler (2010) indicated that the estimate is based on 13 sightings from both linear and non-linear transects, including multiple counts of the same groups over five months, and then extrapolated without habitat variable controls. Regardless, Phong Nha-Ke Bang contains the largest remaining population of red-shanked doucs in Vietnam.

Site 6– Quang Trach District in Quang Binh Province. In 1960, one douc was reportedly hunted in the nearby mountains (Nadler et al., 2003).

Site 7– Vinh Linh District in Quang Tri Province. In 1997, one douc was confiscated in the district (Nadler et al., 2003).

Site 8– Bach Huong Hoa Nature Reserve in Quang Tri Province is 25,200 ha of which 20,646 ha are forested with predominantly secondary tropical evergreen forests below 600 m and subtropical mid-montane forests above 600 m, and it includes limestone karst with elevations ranging up to 1,700 m (Mahood & Tran Van Hung, 2008). This reserve is near the Laos border. Mahood & Tran Van Hung (2008) reported that one to two sightings of doucs were made each year between 2004 and 2006, each sighting was a single event, and contained between three and 30 individuals. Hunting is noted as a threat with biodiversity being considerably reduced in recent years. Illegal logging, mining, and other extractive activities are also documented as a threat and regular occurrences (Mahood & Tran Van Hung, 2008).

Site 9– Da Krong Nature Reserve and Phong Dien Nature Reserve in Quang Tri and Thua Thien-Hue Provinces. These two nature reserves are directly adjacent to each other. Comprising 40,526 and 41,548 ha respectively, their forests are heavily disturbed and extensively deforested, although the largest remaining tracts of primary lowland evergreen forests in the Annamites are found in this area with elevations ranging up to 1,615 m (Birdlife International Sourcebook, 2004). Nguyen Manh Ha (2005) reported one group of 34 individuals. WWF's Green Corridor project reported 10 groups in the area, the largest two of which contained 17 and 14 individuals (Dickson & Van Ngoc Thinh, 2006; Tran Minh Hien & Dickson, 2007; Van Ngoc Thinh et al., 2007). The group which contained 14 individuals was believed to be the same group reported by Nguyen Manh Ha, indicating possible population decline. Hunting and illegal logging were noted as significant problems (Tran Minh Hien & Dickson, 2007; Van Ngoc Thinh et al., 2007).

Site 10– Bach Ma National Park in Thua Thien-Hue Province is 22,030 ha with lowland evergreen and montane evergreen forests, and elevation range from sea level to 1,448 m (Birdlife International Sourcebook, 2004). Groups between three and 25 individuals have been reported over the last 20 years, and each report usually contains a single sighting of a single group (Nadler et al., 2003). Lippold (1998) reported several sightings of groups but the population is not estimated. The most recent survey by Le Thi Dien et al. (2010) reported only 22 to 26 doucs remaining in Bach Ma National Park. Nadler et al. (2003) and Van Ngoc Thinh et al. (2007) noted hunting and illegal logging as threats.

Site 11– Nam Dong District in Thua Thien-Hue Province. Located outside and south of Bach Ma National Park, a single group of 50 to 60 doucs was reported in 1990, and by 2003 this group was suggested to be reduced to 10 individuals (Nadler et al., 2003).

Site 12– Hai Van Pass in Thua Thien-Hua and Da Nang Provinces. The Hai Van pass area (10,850 ha) is not a protected area, although status as a cultural and historical site is proposed (Birdlife International Sourcebook, 2004). Large-scale hunting combined with forest degradation and fragmentation has left visible impacts on the Hai Van range (personal observation, 2008 through 2013). Birdlife International Sourcebook (2004) noted that the natural forests were extensively cleared by chemical defoliants and timber extraction during the Vietnam-American war. In 2009 a Hai Van Pass Ranger (Mr. Thuy) indicated that at least one douc group was still in the area and claimed he observed them on a regular basis. I did not observe doucs but I did hear gibbons calling in the area on one occasion, and we were involved the confiscation of a critically endangered Edward's Pheasant (*Lophura edwardsi*) from a local hunter. It is possible that doucs remain in the Hai Van area as Mr. Thuy suggests, considering other endangered wildlife (gibbons, Edward's Pheasant) were observed there.

Site 13– Ba Na-Nui Chua Nature Reserve in Da Nang Province is 38,210 ha, the forests are mostly lowland evergreen or lower montane evergreen and heavily disturbed, and elevation ranges up to 1,487 m (Birdlife International Sourcebook, 2004). The area was previously owned by logging companies, and was also logged and defoliated during the Vietnam-American war (Birdlife International Sourcebook, 2004). Ba Na-Nui Chua is adjacent to Hai Van Pass but isolated from Bach Ma by a series of lowlands and fragmented forests. Douc sightings have not been reported, although a confiscation suggests a douc population was present in 1999 (Nadler et al., 2003).

Site 14– Son Tra Nature Reserve in Da Nang Province is 2,670 ha; the forests are mostly secondary lowland evergreen with elevations ranging up to 696 m (Birdlife International Sourcebook, 2004; Vietnam Conservation Fund, 2009). Son Tra Nature Reserve is the research site for my study. Doucs were reported here by Van Peenen (1969) and Van Peenen et al. (1971), which represent the first quantifiable records. Various surveys indicated population numbers were low or that the population was extinct until Vu Ngoc Thanh et al. (2007) reported a population of 198 doucs. This was confirmed by Dinh Thi Phuong Anh et al. (2010). Son Tra is completely isolated from the Hai Van Pass by Da Nang City (see Chapter 3). The population here is the second largest known population in Vietnam, and thus of critical importance to survival of the species. Son Tra is discussed in greater detail in Chapter 3.

Site 15– Song Thanh Nature Reserve in Quang Nam Province. Son Thanh Nature Reserve is 93,248 ha. It is dominated by lowland evergreen forests which are disturbed, and elevations range up to about 1000 m (Birdlife International Sourcebook, 2004). It is located along the Laos border. In Song Thanh Nature Reserve one group of doucs was sighted in 1999 (Nadler et al., 2003). Ha Thang Long (2000) noted that hunters are familiar with both red-shanked doucs and grey-shanked doucs, suggesting that the distribution of red-shanked and grey-shanked doucs overlaps in the area. According to Vietnam Conservation Fund’s Project Leader, Dr. Wilfried Butzler (personal communication, 2012), Song Thanh Nature Reserve is under severe threats from hunting, illegal logging and mining.

Site 16– Mom Ray National Park in Kon Tum Province is 56,621 ha, the forest is predominately lowland evergreen and lower montane evergreen, and elevation ranges between 200 and 1773 m (Birdlife International Sourcebook, 2004). Mom Ray is also located along the Laos boarder, and near the Cambodian border. Lippold et al. (2011) represents the only report on doucs in the area, including observations on one group of red-shanked doucs, observations on two *Pygathrix* groups of unidentified species, and observations of potential hybrid doucs. They also have interview data confirming red-shanked doucs and suggesting the presence of black-shanked and grey-shanked doucs. This area represents one of the few areas of potential overlap between all *Pygathrix* species.

Site 17– Kon Ha Nung in Gia Lai Province. This area overlaps Kon Cha Rang Nature Reserve and Kon Ka Kinh National Park. Kon Cha Rang Nature Reserve is located along the coast, it is 15,900 ha which are forested with minor disturbance, the forest is lower montane evergreen with elevations between 800 and 1452 m (Birdlife International Sourcebook, 2004). Kon Ka Kinh National Park is 41,780 ha, the forest varies from montane subtropical evergreen to coniferous and most of the protected area retains natural forest cover with elevations ranging between 570 to 1784 m (Birdlife International Sourcebook, 2004). All three species of doucs have been reported in the area (see Lippold, 1998; Nadler et al., 2003). However, Ha Thang Long (2009) does not report observing red-shanked or black-shanked doucs in his long-term field research on grey-shanked doucs at Kon Ka Kinh National Park.

Laos– based on interview data, status reports and surveys in Timmins & Duckworth (1999) and Coudrat et al. (2012), the population of red-shanked doucs in Laos is larger than in Vietnam, it is less fragmented, but hunting pressures are just as, if not more, significant.

Cambodia– Rawson & Roos (2008) reported sightings of red-shanked doucs in the northeast tip of Cambodia which is consistent with their distribution in adjacent Laos. This is an area of overlap between red-shanked and black-shanked doucs.

Figure 2.6. Distribution sites of *P. nemaeus* in Vietnam. (see Table 2.5 for site names).

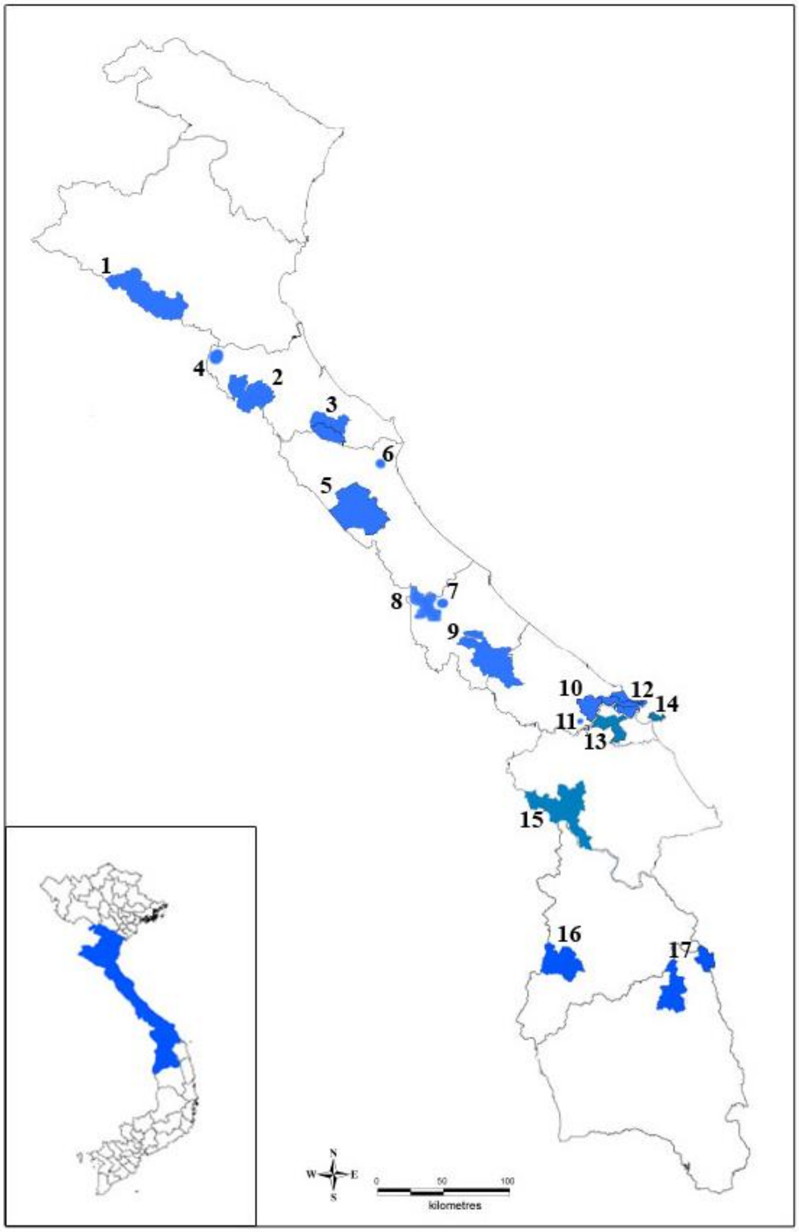


Table 2.5. Distribution sites of *P. nemaeus* in Vietnam (see Figure 2.6 for site map).

Number (on map)	Site Name	Doucs confirmed in last 6yrs	Doucs confirmed 7-25 yrs ago	Interviews, specimens, confiscations	Population estimate / population notes
1	Pu Mat National Park		▨		Last sighting in 1993-1996; 25 to 31 individuals
2	Vu Quang National Park		▨		Last sighting in 2000
3	Ke Go Nature Reserve			▨	Interview data in 1996
4	Site in Huong Son District		▨		Last seen in 2000
5	Phong Nha-Ke Bang National Park	▨			445 to 2137 individuals (2009)
6	Site in Quang Trach District			▨	Specimen in 1960
7	Site in Vinh Linh District			▨	Confiscation in 1997
8	Bach Huong Hoa Nature Reserve	▨			Last seen in 2006; 3 to 30 individuals
9	Dakrong Nature Reserve and Phong Dien Nature Reserve	▨			10 groups reported in 2007
10	Bach Ma National Park	▨			22 to 26 individuals observed in 2010
11	Site in Nam Dong District		▨		10 individuals seen in 2003
12	Hai Van Pass area			▨	Interview in 2009
13	Ba Na-Nui Chua Nature Reserve			▨	Interview and confiscation in 1999
14	Son Tra Nature Reserve	▨			198 to 208 individuals reported in 2007 and 2010
15	Song Thanh Nature Reserve, Hien District and Nam Giang District			▨	Interview in 1999
16	Mom Ray National Park	▨			One group observed in 2011
17	Kon Cha Rang Nature Reserve and Kon Ka Kinh National Park		▨		Possible red-shanked doucs seen in 1998

2.5.2. Population size and status

As of 2013 there is no reliable population estimate for the red-shanked doucs (IUCN, 2012; Liedigk et al., 2012; Vu Ngoc Thanh et al., 2008). The only estimate given was based on available forest cover in Southeast Asia and assumed *Pygathrix* distribution in 1987. MacKinnon & MacKinnon (1987) estimated that there were up to 72,720 individual *Pygathrix* remaining the wild. This estimate was adjusted to account for non-protected areas, and they estimated the number of protected *Pygathrix* individuals at 9,150 individuals. This estimate is low. Pollard et al. (2007) and Clements et al. (2008) estimated the black-shanked douc population in the Seima Biodiversity Conservation Area of Cambodia at 42,603 individuals alone, although recent survey estimates by Wildlife Conservation Society at this site suggest around 24,000 individuals (Nuttall, 2013). For the Vietnamese endemic grey-shanked doucs, the current estimate is below 1000 individuals (Nadler, 2010), and likely between 550 and 700 individuals (Liedigk et al., 2012). For the Laos red-shanked douc population, Coudrat (2013) estimated 2.8 groups of doucs per km^2 in the Nakai-Nam Theun National Protected Area alone.

I offer a speculation about the population numbers of red-shanked doucs in Vietnam and throughout their distributional range- 1000 to 2000 individuals in Vietnam and a population of at least 3 to 5 times that in Laos. Although these numbers are speculative, the previous review of the status of red-shanked populations in Vietnam shows that all locations from which red-shanked doucs have been reported contain small and possibly extirpated populations, aside from Son Tra Nature Reserve (198-208 individuals), and Phong-Nha Ke Bang National Park (445-2137 individuals).

Given the small population size based on all available evidence, red-shanked doucs are classified as Endangered by IUCN Red List (2012) under criteria A2cd, 3cd and 4cd of version

3.1, and are classified as Endangered by Vietnam's Red Data Book (MOSTE, 2000). The IUCN classification is based on a) a decline in population numbers of 50% or more in the last 30 to 36 years, b) the reason for this decline is related to habitat loss and hunting pressure and c) the decline in population is predicted to continue at this same rate or even higher over the next 30 to 36 years.

2.6. Socioecology

2.6.1. Approaches in understanding socioecology and feeding ecology

Influences of weather (temperature and precipitation), habitat (quality, phenology, disturbance), and plant quality (chemical, nutritional, physical, seasonality) on behavior (activity budgets, feeding, ranging) represent aspects of socioecology. Socioecology studies are useful in developing conservation practices (Fashing, 2007b; Hoang Minh Duc, 2007; Nijman, 2010).

Parga & Overdorff (2011) described socioecology as the influence of phenology, group size, composition, territoriality, mating, ranging, activity, and feeding ecology on social ecology. Phenology is the description of forest habitat vegetation and its fluctuations (Ganzhorn, 2003). According to Robbins & Hohmann (2006: 1), feeding ecology relates to "survival, reproduction, population dynamics, habitat requirements, and patterns of sociality." Aspects of feeding ecology include nutritional ecology, which is the interplay between plant nutrition and chemistry, spatial and temporal variations in food availability and quality, and food selection (Janzen, 1978; Lambert, 2011; McKey, 1978; Milton, 2006; Robbins & Hohmann, 2006; Rode et al., 2003; Yeager et al., 1997). Feeding ecology studies also overlap with sensory ecology (Dominy et al., 2001; Hladik & Simmen, 1996; Lucas et al., 1995; Lucas et al., 1997; Lucas et al., 2000; Lucas et al., 2001; Strait, 1997; Unger, 1995), and studies of phenology, habitat type, and seasonality (Agetsuma, 2000; Agetsuma & Noma, 1995; Chapman & Chapman, 1999; Cords, 1987;

Fashing, 2001b; Harris & Chapman, 2007; Kaplin & Moermond, 2000; Milton, 1980; Strier, 1991; Silver et al., 1998).

Leaves represent the most abundant dietary item and a primary source of protein for folivorous primates, but they are difficult to digest (Montgomery, 1978; Waterman, 1984). As leaves mature protein levels decline and fiber levels increase (Coley and Aide, 1991). Folivorous primates should therefore prefer young leaves to mature leaves, a prediction which is frequently supported among colobines (see Zhipang Huang et al., 2010; Milton, 1979; Milton, 1998; McKey et al., 1981; Mowry et al., 1996; Nguyen Thi Tinh et al., 2012; Oates, 1988a; Oates et al., 1977; Otto, 2005; Wasserman & Chapman, 2003; Yeager, 1989; Yeager et al., 1997).

Colobines are noted for including a large portion of leaves in their diet than other primates (Kirkpatrick, 2011; Napier & Napier, 1970; Oates, 1987; Oates & Davies, 1994). Plants contain compounds that reduce digestibility (*i.e.*, fibers), or target physiological pathways (*i.e.*, toxic compounds) (Belovsky & Schmitz, 1994; Freeland & Janzen, 1974; Yeager et al., 1997). Plant compounds have been argued to influence foraging decisions (Kirkpatrick et al., 1998). Colobine digestive systems allow for efficient nutrient extraction and detoxification of secondary compounds in leaves (Bauchop, 1978; Gaulin, 1979; Hladik, 1977; Kay & Davies, 1994; Oates & Davies, 1994; Oates et al., 1977; Waterman et al., 1988; Yeager et al., 1997). Colobines should therefore be less concerned with selecting foods based on secondary compound content, a prediction which is also largely supported among colobines (Burgess & Chapman, 2005; Chapman & Chapman, 2002; Davies et al., 1988; Fashing, 2001a; Hoang Minh Duc et al., 2009; Maisels et al., 1994; Nijman, 2010; Oates et al., 1980; Pages et al, 2005; Steel, 2012; Wasserman & Chapman, 2003; Waterman & Kool, 1994; Workman, 2010a).

Numerous studies relate colobine biomass to the quality of foliage (Brugiere et al., 2002; Chapman & Chapman, 1999; Chapman & Chapman, 2000a; Chapman et al., 2002; Davies et al., 1988; Fimbel, 1994; Ganzhorn, 1992; Gogarten et al., 2012; McKey, 1978; Milton, 1978; Oates et al., 1977; Plumptre & Cox, 2006; Yeager et al., 1997). Chapman et al. (1999) and Oates et al. (1990) noted biomass is also affected by hunting, habitat quality, seasonality, competition, disease, and historical or catastrophic events. Anthropogenic influences (e.g. hunting, habitat destruction) have a more immediate and significant influence on primate biomass (Fashing, 2007; Struhsaker, 1997).

Studies of seasonal variation in plant productivity illustrate the influence of seasonality on primate behaviors (Altmann & Altmann, 1970; Brugiere et al., 2002; Hohmann et al., 2006; Manly et al., 2002), and ranging, activity and foraging decisions are often related to resource abundance and distribution (Agetsuma & Noma, 1995; Russo & Chapman, 2011).

2.6.2. Protein, fiber, and tannins

National Research Council (NRC, 1978; NRC, 2003) analyzed the role and requirements of nutrients for non-human primates. NRC (2003) recommended minimal daily intake of nutrients and minerals for colobine primates are provided in Table 2.6, which are given as percentage of Dry Matter Basis or milligram per kilogram of body mass. Differences in recommended daily value between primate species and across life stages are likely to exist, however this has not been established for most non-human primate species.

Table 2.6. Daily recommended nutrient intake in colobines.
(Adapted from NRC, 2003)

Nutrient	Recommendation
Crude Protein	15-22%
NDF	10-30%
ADF	5-15%
Ca	0.8%
P	0.6%
Mg	0.08%
K	0.4%
Na	0.2%
Fe	100 mg/kg
Cu	20 mg/kg
Mn	20 mg/kg
Zn	100 mg/kg

2.6.2.1. Protein

NRC (2003) reported protein requirements for ceropithecid primates are between two and four grams of protein per kilogram of body weight per day. Protein-to-fiber ratios of mature leaves influence the abundance of colobine primates within a habitat (Brugiere et al., 2002; Chapman et al., 2002; Fashing, 2007; Fashing & Cords, 2000; Milton, 1978; Oates et al., 1990), and therefore the quality of fall-back foods influences biomass.

2.6.2.2. Fiber

Fiber is related to the cell walls of plant tissues (Mohsenin, 1970), and consists of cellulose, hemicellulose, and lignin. Unlike cellulose, hemicellulose is not resistant to hydrolysis, although both are indigestible without anaerobic bacterial fermentation (Waterman & Kool, 1994), which is why colobines are able to subsist on low quality (high fiber) foods. Lignins are polyphenols that are indigestible and unfermentable (NRC, 2003). Colobine foods on average consist of about 44% neutral detergent fiber (NDF) of dry matter and 34% acid detergent fiber (ADF) of dry matter (NRC, 2003). Neutral detergent fiber includes the total insoluble fiber in plant cell walls, which is primarily cellulose, hemicellulose, and lignin. Acid detergent fiber is a measure of cellulose and lignin. As noted in the review of colobine digestive anatomy, fiber is important to maintain healthy pH levels in the forestomach (Lambert, 1998; Milton, 1984a) and general gastrointestinal health (Edwards & Killmar, 2004). Fiber has been shown to be a critically absent dietary component of captive red-shank doucs (Edwards & Killmar, 2004).

2.6.2.3. Phenolics and toxins

Secondary compounds (fiber and phenolics) are part of a plant's defensive strategy. Secondary compounds can be divided into two general categories; digestion inhibitors and toxins (Lambert, 1998; Waterman & Kool, 1994). Phenolics include tannins, which are a digestion inhibitor, and a polyphenolic compound that interferes with uptake of animal protein by binding with plant proteins to form insoluble complexes (Dominy et al., 2001; Lambert, 1998; Lucas et al., 2003). Studies have shown that the presence and quantity of condensed tannins in plant foods can negatively affect primate feeding (Glander, 1981; Glander, 1982; McKey et al., 1981; Oates et al., 1977) and can lead to toxicity (Dominy et al., 2001). Saliva of some primates contains proline rich proteins which bind to tannins allowing for the uptake of plant proteins (Lambert, 1998). As noted above, this may characterize colobine primates. Waterman & Kool (1994) observed that some tannins can neutralize plant toxic defenses, and thus are beneficial.

Toxic compounds such as alkaloids and cyanogenic glycosides are absorbed in the gastrointestinal tract and have a toxic effect on the consumer (Lambert, 1998). Freeland & Janzen (1974) showed primates reduce the effects of toxic compounds through microbial activity and microsomal enzymes. Among colobines some toxic secondary compounds can be broken down by bacterial activity which is supported in the anaerobic alkaline stomach environment (Lambert, 1998). Additionally, some toxic compounds might be selected as a means to remove internal parasites (Rodriquez et al., 1985).

2.7. Diets of colobines

There is a wide range of variation and dietary adaptations among colobines. Diets may be characterized by a high intake of young leaves (Kool, 1989; Oates, 1988a; Struhsaker, 1975) or mature leaves (Newton, 1992; Stanford, 1991), seeds (Harrison, 1986; McKey et al., 1981), fruits (Starin, 1991), and some even subsist seasonally on lichen (Bleisch et al., 1993; Bleisch & Jiahua Xie, 1998; Li Yiming, 2006; Songtao Guo et al., 2007).

Colobine diets are seasonal (Davies & Oates, 1994; Fashing, 2011; Kirkpatrick, 2011), and food selection is influenced by food quality (Fashing, 2007). It is an over-simplification to classify the colobine radiation as folivorous or as "leaf-eating monkeys" (Fashing, 2007; Oates, 1994; Waterman & Kool, 1994), which refers to morphological adaptations to folivory rather than actual diet. Studies in the last 10 years have added to a growing understanding of *Pygathrix* and the odd-nosed colobines.

2.7.1. Diets of African colobines – general patterns

For African colobines, young leaves are generally important in their diet, and mature leaves are often exploited as a fall-back resource. Diversity abounds. *Procolobus* is generally folivorous and prefer young leaves, some *Colobus* populations select fruits or seeds in large amounts and some rely on lichen seasonally, and some *Piliocolobus* populations consume fruits or seeds or flowers as often as young leaves. In some instances, food species availability is low and therefore dietary species diversity is low, but not always (Fashing, 2001a; 2011). Food availability influences diet in some species, but not all (Davies et al., 1999). Selection may be influenced by fiber or protein content in leaves and fruits, but the importance of fruit or young leaves in the diet can differ between and even within species, as does the influence of protein, fiber, or even tannins (Davies et al., 1999; Fashing, 2001a; Fashing, 2011; McKey et al, 1981; Oates et al., 1977).

See Table 2.7 for a summary of our current understanding of African colobine diets. For specific information outlined in Table 2.7 see Baranga (1983), Booth (1956), Brugiere et al. (2002), Chapman & Chapman (1999; 2000a; 2002), Clutton-Brock (1975), Cooney & Struhsaker (1997), Danish et al. (2006), Dasilva (1989;1994), Davies et al. (1999), Decker (1994), Dominy & Lucas (2004), Dunbar & Dunbar (1974), Fashing (2001a; 2011), Fashing et al. (2007a), Fimbel et al. (2001), Gatinot (1977), Gautier-Hion et al. (1997), Harris & Chapman (2007), Harrison (1986), Lowe & Sturrock (1998), Maisels et al. (1994), Marsh (1981a), McKey & Waterman (1982), McKey et al. (1981), Mowry et al. (1996), Mturi (1993), Nowak (2008), Oates (1978; 1988a; 1994), Oates et al. (1977), Rode et al. (2003), Ryan et al. (2012b), Saj & Sicotte (2007a), Starin (1991), Steel (2012), Struhsaker (1975), Struhsaker et al. (1997), Usongo & Amubode (2001), and Wasserman & Chapman (2003).

Table 2.7. Diets of African colobines.

Species	Percentage of time spent selecting food parts in annual diet						
	%Total Leaves	Young Leaves	Mature Leaves	Fruit	Seeds	Flowers	Other
Colobus angolensis	38-72	25-30	2-40	17-28	20-22	1-7	6-37
C. guereza	53-87	24-81	4-25	5-39	1-22	1-9	0-15
C. polykomos	49-58	28-30	20-26	35-48	32	3	1-3
C. satanas	26-38	21-35	3-18	50-64	41-60	3-12	0-5
C. vellerosus	79	40	34	15	4	6	0
Piliocolobus badius	31-76	24-70	4-20	19-42	3-25	1-30	1-9
P. gordonorum	74	46	15	5	15	3	3
P. epieni	66	56	10	16	12	9	9
P. kirkii	63-67	50-55	7-9	5-32	0-2	5-8	0-22
P. pennantii	76-87	58-72	5-16	6-14	--	2-7	2-10
P. preussi	89	89	0	1	--	10	0
P. rufomitratus	47-65	46-61	1-11	22-26	1	6-27	1-4
P. tephrosceles	73-92	35-79	7-44	5-11	1-2	1-16	1-7
P. tholloni	61	54	6	38	31	1	0
Procolobus verus	74-85	59-83	1-11	8-19	14	4-7	0-3

2.7.2. Diets of Asian colobines

2.7.2.1. General patterns

Diets among Asian colobines are equally diverse. Asian colobines are primarily folivorous with seasonal diets characterized by a rainy frugivorous season and dry folivorous season, although this does not characterize the entire radiation. Generally, mature leaves are exploited as a fall-back resource. Seasonal shifts in diet can be extreme among some species and the percentage of young leaves in the diet varies greatly. Foods lower in fiber or enriched in protein are generally preferred. Certain *Presbytis* species exploit high amounts of seeds when available. Some *Presbytis* species primarily select fruits and young leaves compared to the high intake of mature leaves in other species (Bennett & Davies, 1994). Among *Trachypithecus*, *Nasalis* and *Pygathrix* some species exploit young leaves over mature leaves, and fruits or seeds over young leaves. *Rhinopithecus* species have some of the most distinctive colobine diets related to the temperate climates in which they live, including food resources such as lichens and bark. For *Pygathrix* species, our understanding of their diets has increased exponentially in the last six years.

Table 2.8 provides an overview of Asian colobine diets. Odd-nosed colobines are reviewed in greater detail below. For specific information outlined in Table 2.8 see Bennett (1983), Curtin (1980), Davies (1991), Davies & Baillie (1988), Davies & Bennett (1988), Davies et al. (1988), Fuentes (1996), Gurmaya (1986), Hadi et al. (2012), Hladik (1977), Kirkpatrick (2011), Koenig et al. (2004), Kool (1989; 1992; 1993), Kullik (2010), Newton (1992), Nijman (2010), Oates et al. (1980), Pages et al. (2005), Quhai Zhou et al. (2006), Ruhiyat (1983), Solanki et al. (2008), Stanford (1991), Steenbeek & van Schaik (2001), Sugiyama’s (1976), Supriatna et al. (1986), Workman (2010a; 2010b), and Workman & Le Van Dung (2010).

Table 2.8. Diets of Asian colobines. Based on above references. Data from this study is not included but compared in chapter 7.

	Percentage of time spent selecting food parts in annual diet					
Species	%Total Leaves	Young Leaves	Mature Leaves	Fruit/ Seeds	Flowers	Lichens/ Fungus	Other
Semnopithecus dussumieri	39-49	4-14	35	24	10	--	3-11
S. ajax	58	--	--	29	7		2-4
S. priam	48	27	21	45	7	--	--
Trachypithecus vetulus	60	20	40	28	12	--	--
T. johnii	52	25	27	25	9	--	13
T. auratus	56	46	<10	32	14	--	8
T. obscurus	57	36	21	36	7	--	--
T. p. leucocephalus	83-89	75	8-11	2-3	6-8	--	2
T. pileatus	53	11	42	34	7	--	5
T. phayrei	--	39	--	36	--	--	--
T. delacouri	78-80	58-60	20	9-10	5	--	6-7
T. francoisi	53	39	14	31	8		7
Presbytis femoralis	29	26	3	58	<1	--	13
P. siamensis	35-36	24-28	8-11	49-56	6-12	--	2-3
P. comata	65	59	6	14-27	7	4	8
P. thomasi	36-43	--	--	41-53	8	--	3
P. hosei	66-78	45	5	19-28	3	--	6
P. rubicunda	37-38	37	1	49-52	11-12	--	2
P. potenziani	55	--	--	32	--	--	13
Simias concolor	--	--	--	--	--	--	--
Nasalis larvatus	41-74	38-73	<1-10	11-58	3-8	--	0-8
Rhinopithecus bieti	>6-34	16	5	1-11	1	60-86	7-8
R. roxellana	24-32.5	29	3.5	15-29	--	29-43	1-13
R. brelichi	48-71	26	22	15-22	7	0.2	6
R. avunculus	33-38	11-38	--	47-63	8	--	3
Pygathrix nemaeus	63-82	75	7	14-37	4	--	--
P. cinerea	59	50	9	41	0.1	--	0.1
P. nigripes	40-54	24	6	29-52	12-15	--	0.1-1

2.7.2.2. Odd-nosed colobines

2.7.2.2.1. *Siamas, Nasalis,* and *Rhinopithecus*

Siamas concolor– Hadi et al. (2012) reported on the diets of the pig-tailed snub-nosed monkey (*Simias concolor*) from Mentawai Islands, Sumatra. Diet was diverse with 99 plants species, the top 10 of which accounted for 48% of the diet. Although no comparable numbers were presented, leaves were exploited most frequently according to time, followed by fruits and then flowers. Considering the possible 100% territory overlap between *S. concolor* and *Presbytis potenziani* groups, differences in dietary species and the high degree of dietary diversity among both species may be factors permitting for significant home range overlap.

Nasalis larvatus– the proboscis monkeys (*Nasalis larvatus*) are a good example of multiple populations of a single species exhibiting different food preferences and exploiting food in different percentages. Bennett & Sebastian (1988) reported the *N. larvatus* in Sarawak, Borneo, fed mostly on seeds, fruits and young leaves with mature leaves accounting for only 3% of the diet. They suggested home ranges were large because preferred foods were not abundant. Yeager (1989) reported *N. larvatus* preferred fruits & seeds (40%) and young leaves (~41%), both of which were selected according to availability. During times of preferred food scarcity they increased ranging and the species diversity of plant foods eaten. Matsuda (2008) also noted that feeding was influenced by availability, and that young leaves were selected most often (66%), followed by fruits and seeds (26%) and flowers (8%). Yeager et al. (1997) reported young leaves were preferred and had higher concentrations of protein, phosphorus, potassium, and zinc compared to mature leaves. Matsuda et al. (2009a) reported fruits were preferred and young leaves were only a high quality fall-back resource.

Rhinopithecus bieti– Wei Ding & Qi-kun Zhao (2004) reported the Yunnan snub-nosed monkey (*Rhinopithecus bieti*) from Tacheng, Yunnan fed mostly on lichens (60%), with dicot and bamboo leaves comprising much of the remaining diet. Zuo-Fu Xiang et al. (2007) illustrated *R. bieti* from Xiaochangdu, Tibet, also fed predominantly on lichens (75%) followed by leaves & buds (16%), fruits & flowers (2%), invertebrates (2%), and resins and bark (5%). Long Yongcheng & Kirkpatrick (1991) reported *R. bieti* fed mostly on grass and lichens, which was supplemented by bark in the winter and young leaves and fruits in the summer. Grueter et al. (2010) reported lichens were the most commonly selected food (67%), followed by young leaves and buds (16%), fruit and seeds (11%) and mature leaves (5%). Dietary diversity was low and the top 10 food species accounted for more than 90% of the diet. Long Yongcheng et al. (1998) also found that lichens (up to 91% seasonally) are important in the diet. Diets of *R. bieti* are not as seasonal compared to other Chinese *Rhinopithecus* species; lichens remain a constant dietary component. Zhipang Huang et al. (2010) found that leaves selected by *R. bieti* were lower in fiber content than non-selected leaves, but protein content did not differ.

Rhinopithecus roxellana– From the Qinling Mountain in China, Songtao Guo et al. (2007) reported the golden snub-nosed monkey (*Rhinopithecus roxellana*) selected fruits and seeds (29%), lichens (29%) and leaves and buds (28%) most frequently, with bark (11%) and twigs (2%) comprising the remainder of food items. Ranging increased with abundance of fruits and seeds, and diets are diverse and seasonal (Kirkpatrick, 1998; Songtao Guo et al., 2007). Winter diets vary between sites, and consist of bark, pine nuts, buds or lichens in varying degrees (Kirkpatrick, 1998). Li Yiming (2006) found diets in Shennongjia Nature Reserve were dominated by lichens (43%), but young leaves (29%) and fruits & seeds (15%) were preferred. Mature leaves (3.5%) and bark (1%) were rarely selected. In contrast, Su Yanjie et al. (1998) reported bark eating was common in winter for this same population. Finally, Xuecong Liu et al. (2013) reported selected lichens contained higher amounts of water soluble carbohydrates and similar values of fat to selected leaves, in addition to low fiber content than selected mature leaves, fruits and flowers.

Rhinopithecus brelichi– Bleisch et al. (1993) reported diet of the Guizhou snub-nosed monkey (*Rhinopithecus brelichi)* is dominated by leaves and buds from broad leaf trees. Zuo-Fu

Xiang et al. (2012) described *R. brelichi* diet as diverse and seasonal, with young leaves (26%), mature leaves (22%), and fruits and seeds (22%) dominating the diet at different times of the year. Bleisch & Jiahua Xie (1998) reported a low diversity of food species but diets were highly seasonal. Spring was dominated by consumption of young leaves (93%), winter was dominated by buds (90%), and fruits and seeds were selected in high frequency in the summer and autumn. Bleisch et al. (1998) noted young leaves did not differ in protein or fiber content from non-selected leaves, and selected fruit contained less protein then selected leaves.

Rhinopithecus avunculus– Pham Nhat (1994b) estimated the diet of the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*) to be 37% leaves and 63% fruits. Boonratana & Le Xuan Canh (1998) observed that *R. avunculus* in Na Hang fed mostly on unripe fruits (47%) and young leaves (38%). Le Khac Quyet et al. (2007) reported that fruit (47%) was a significant part of the diet, as were leaf petioles (22%). Young leaves (11%), flowers (8%), seeds (5.5%) and pith (3%) comprised the remainder of the diet. They also suggested that *R. avunculus* is a highly selective forager with a low dietary diversity.

2.7.2.2.2. *Pygathrix*

In *Primates in Perspective*, the detailed dietary tables report nothing on the diets of *Pygathrix* (Kirkpatrick, 2011). Our knowledge of food selection and dietary influences relating to *Pygathrix* would appear absent. Twenty years ago, the compendium of colobine feeding ecology by Bennett & Davies (1994: 164) noted “the behavior and ecology of wild *Pygathrix* is almost totally unknown”. At the start of this study, Fleagle (1999: 219) summarized the state of knowledge of *Pygathrix* in five sentences, in which he mentioned, “Little is known about their natural behavior.” Although some updated ecological information about *Pygathrix* is provided in Fleagle (2013), it still appears that little is known about this genus. Review of dietary information in the 2002 Vietnam Primate Conservation Status Review on Leaf Monkeys for red-shanked doucs consists of two sentences, and stresses the importance of understanding ecology for developing sustainable primate conservation initiatives (Nadler et al., 2003). Over the last six years a number of studies have begun to fill this void.

Several studies have reported on diets of red-shanked doucs in wild or captive settings, two long-term studies have reported on the diets of black-shanked doucs, and one long-term study has reported on the diet of grey-shanked doucs. The current state of knowledge of *Pygathrix* feeding ecology is reviewed in chronological order rather than according to species.

The first wild study on a species of *Pygathrix* was on red-shanked doucs on Son Tra Nature Reserve, Vietnam (Lippold, 1977). It was reported that feeding concentrated on young leaves and suggested that fruit availability might influence ranging. While she reported that she never saw red-shanked doucs on the ground Van Peenen et al. (1971) noted that doucs were seen on the ground when the ridge road on Son Tra Nature Reserve was newly constructed in the mid 1960’s.

Pham Nhat (1993a) estimated the diet of red-shanked doucs to be 63% leaves and 37% fruits. A detailed analysis by Pham Nhat (1994a) compiled data from various locations in Vietnam including Ha Tinh Province in 1985, Son Tra Peninsula in 1988, and Mad Rak in 1992. Field observations from these studies were combined with analysis of stomach contents from five individuals. Diet consisted of leaves, buds, flowers, fruit, and bamboo shoots. There were 50 recorded plant species eaten from 21 different families. The analysis was largely based on stomach contents so additional information involved in selection could not be intuited. Of the 50 different plant species identified, 26 were exploited for leaves, 41 for fruits, four for bamboo shoots, four for buds, and three for flowers, with most plant species being exploited for more than one food category. His study suggested a diverse diet and that fruit was an important dietary component.

Lippold (1998) reported dietary data from four years of surveys in Vietnam. Results indicated that red-shanked and black-shanked doucs were highly folivorous; exploiting young leaves (75%) and fruits and seeds (14%) frequently, followed by mature leaves (7%) and flowers (4%). She suggested that *Pygathrix* were more folivorous than indicated by Pham Nhat (1993a; 1994a), and noted Moraceae as an important resource.

The National Research Council (NRC, 2003) reported the diets of *Pygathrix* species consist of 37% young leaves and buds, 37% mature leaves, 15% fruits, 3% seeds, 7% flowers, and 5% lichens. Figs were noted as being an important food resource. Because citations are lacking, it is unclear where these figures are from.

Otto (2005) reported on the diets of red-shanked doucs at the Cologne Zoo, Germany and the Endangered Primate Rescue Center (EPRC), Vietnam. Her study was only 10 days at the EPRC and unfortunately lacked basic methodological controls and quantitative analyses. However, her study was until recently the most exhaustive on the diets of *Pygathrix*, and is therefore often referenced. She reported feeding mostly on young leaves. Nutritional analyses revealed that young leaves were enriched in protein and lower in fiber than mature leaves. Mature leaves of one species were selected frequently and these leaves had higher protein and lower fiber content compared to other mature leaves. Tannin content did not differ between selected and non-selected plants. The EPRC diet was enriched in both NDF and ADF compared to the diet in Cologne Zoo. The five least selected plants had the highest fiber content and lowest protein-to-fiber ratios.

O'Brien (2006) and O'Brien et al. (2006) compared dietary aspects of *P. nemaeus* and *P. cinerea* at the EPRC, reporting *P. cinerea* selected foods enriched protein, and although tannin content between select and non-selected foods were not significantly different both *Pygathrix* species tended to avoid foods higher in tannins. Wright et al. (2008a), Ulibarri (2006) and Ulibarri et al. (2006) reported mechanical toughness values (reflecting fiber content) were not significantly different between selected and non-selected foods. However, lower values were among preferred foods.

Hoang Minh Duc was the first scientist to conduct a long-term field study on *Pygathrix* in the wild, paving a new path for *Pygathrix* research and bringing it into accord with current methodologies and debates. Hoang Minh Duc (2007) reported on the feeding ecology of black-shanked doucs (*P. nigripes*) from two wild populations: Nui Chua and Phuoc Binh National Parks, Vietnam. Annual diet consisted of leaves (54%), fruit (19%), seeds (10%), flowers (15%) and other (1%). Young leaves were noted as preferred over mature leaves, and leaves were a significant part of the diet varying between 23% in the wet season to 70% in the dry season. The wet season was characterized by an increased consumption of fruits (34%), and leaves (52%) and flowers (13%) were consumed less frequently than in the dry season. The dry season was characterized by greater leaf (60%) and flower (20%) consumption, with a decrease in fruit (17%) consumption. Petioles of only a single species were consumed. His study illustrated the seasonal importance of fruits and seeds in the diet of black-shanked doucs. Dietary diversity was high among the Nui Chua population with 135 species exploited, and low among the Phuoc Binh population with 39 species consumed. Hoang Minh Duc (2007) and Hoang Minh Duc et al. (2011) reported no statistically significant differences in the protein, fiber, most micronutrient or tannin content between selected and non-selected foods. However, selected foods tended to have higher concentrations of cellulose and lower protein. Hoang Minh Duc (2007) did observe black-shanked doucs on the ground feeding and even standing bipedally to collect food, although these were rare occurrences and only observed during the dry season.

Rawson (2009) further added to the growing knowledge of black-shanked douc feeding ecology with a long-term study in Seima Biodiversity Conservation Area, Mondulkiri, Cambodia. Annually, seeds were a significant part of the diet (40%), followed by young leaves (24%), fruit (12%), flowers (9%), mature leaves (6%), leaves of unidentified age (10%), and other foods (0.1%). The wet season was characterized by a greater consumption of seeds (48%), and leaves (38%) and flowers (4%) were consumed less frequently than in the dry season. The dry season was characterized by increased leaf (42%) and flower (15%) consumption, and lower seed (30%) consumption. His study illustrated the annual importance of seeds in the diet of black-shanked doucs, and that his study groups were not predominantly folivorous. The area was however noted as affected by logging, and selective logging may have resulted in increased seed consumption and decreased leaf consumption. The selection of young leaves, fruits & seeds, and flowers correlated with availability. Dietary diversity was noted as high.

Ha Thang Long (2009) reported on his ongoing long-term study of grey-shanked doucs in Kon Ka Kinh National Park, Gia Lai, Vietnam. Annually, diets were high in young leaves (50%) and fruit & seeds (41%), with the remainder of the diet consisting of mature leaves (9%) and other foods (0.1%). Selection of young leaves and fruits was correlated to availability. The dry season was characterized by increased consumption of young leaves (82%) compared to fruit and seeds (12%) and mature leaves (6%). The wet season was characterized by increased consumption of fruit and seeds (69%), followed by young leaves (18%) and matures leaves (13%). His study illustrated that *Pygathrix* cannot be classified as only folivorous given the seasonal importance of fruits and seeds. Dietary diversity was high with 166 food species recognized, and the top 10 food species comprised 59% of the diet suggesting the doucs are highly selective feeders. Nguyen Thi Tinh et al. (2012) conducted nutrient analysis on select foods from Ha Thang Long's study groups. They reported 135 plant species in the diet, and combined with Ha Thang Long (2009) plant species list the total number of different food species is 251 species. There was no difference in the fiber or protein content of selected young and mature leaves.

Phiapalath (2009) conducted a long-term field study on red-shanked doucs in Hin Namno National Protected Area, Khammouane, Laos. Due to the way in which data were evaluated it is not possible to compare the contribution of major food items (fruits, seeds, leaves, flowers) to their annual diet. Food items were constructed into numerous unique categories forming combinations of major food items, but not major food items separately. It is clear that seeds alone comprise a very low proportion of the diet (1-2%), fruits with or without seed consumption (44%+), and leaves and buds (31%+) are both significant in the diet. Seasonal shifts in diet were not examined although the author suggested that fruit is consumed most when available in the wet season and leaves dominate the diet in the dry season. Phiapalath et al. (2011) reported the dry season involved higher leaf (80%) and lower fruit consumption (9%), compared to the wet season consumption of fruit (54-57%) and leaves (21-39%). Dietary diversity was high; 112 food species. Phiapalath (2009) observed the red-shanked doucs feeding on the ground seven times.

Regarding water intake, Kullik (2010) reported *P. cinerea* in the EPRC meet about 60% of their water requirements through leaf consumption and 40% from active drinking. Lippold (1977) suggested that *P. nemaeus* obtained most water from food intake based on an absence of drinking observations aside from dew licking from leaves. Rawson (2009) observed no water intake. In contrast, Nadler (2008) reported the black-shanked doucs in Hon Heo Peninsula, Vietnam, regularly sit on rocks and drink water from puddles. Typically, terrestrial behavior among *Pygathrix* is rarely observed in long-term studies (see Ha Thang Long, 2009; Hoang Minh Duc, 2007; Rawson, 2009; this dissertation).

Geophagy has been recorded among red-shanked doucs by Rawson & Luu Trong Bach (2011) at a salt lick. This is unique in that it is the first record for geophagy among *Pygathrix*, indicating mineral consumption, pH balancing, toxin buffering, or a combination of these influencing factors.

2.8. Social organization, group size, and composition in colobines

2.8.1. General patterns

There is significant diversity in social organization among African colobines. Adult male to female ratios are typically 1:2, but some species have mainly one-male units, others have two-male units, and others can have even more males within a unit. Males tend to disperse most frequently, although female dispersal is observed for several species. *Piliocolobus* species range widely in their group sizes, from fewer than 10 to over 300 individuals. In areas of increased natural predation there tends to be an increase in group size. Korstjens & Dunbar (2007) suggested that among *Colobus* the major factor affecting group size is digestibility of fall-back foods, and this also influences activity patterns by increasing the time spent resting during the day to allow for digestion. In general, habitats that are more seasonal and disturbed tend to support smaller group sizes than more tropical and undisturbed areas (Fashing, 2011).

Among Asian colobines, adult male to female ratios are typically 1:2 and the basic pattern of organization is the one-male unit (Kirkpatrick, 2011), although there are significant variations on this theme. Yeager & Kirkpatrick (1998) suggested that fusion of one-male units characterizes Asian colobines, and although debate remains it does characterize some Asian colobines. It is common to find multi-male groups and fusion of one-male units to varying degrees, including stable banding through daily fission-fusion. Decreased aggressive interactions between males are found among groups with an increased degree of fusion and fission. Males tend to disperse, although female dispersal is also observed in some species. Group size of one-male units is usually around 13 individuals.

Table 2.9 provides an overview of colobine group size, sex ratio and ranging behavior. Odd-nosed colobines are reviewed in greater detail below. For specific information on the other colobines outlined in Table 2.9 see Bennett (1986), Bishop (1979), Boggess (1979; 1980), Clutton-Brock (1975), Curtin (1980), Dasilva (1989), Davies (1987), Dunbar (1987), Fashing (2011), Fay (1985), Hohmann (1989), Galat & Galut-Luong (1985), Gatinot (1977), Kirkpatrick (2011), Kool (1989), Marsh (1979), Newton (1986; 1987; 1992), Newton & Dunbar (1994), Nijman (2010), Oates (1974; 1977; 1979; 1988a; 1994), Oates et al. (1980), Olson (1980), Ruhiyat (1983), Srivastava et al. (1991), Stanford (1991), Steenbeek et al. (2000), Struhsaker (1975), Struhsaker & Leland (1979), Sugiyama (1976), Supriatna et al. (1986), Tenaza & Fuentes (1995), Tilson & Tenaza (1976), and Wolf & Fleagle (1977).

Table 2.9. Group size, sex ratio, home range, and daily path lengths of colobines. Based on above references. Data from this study are not included but compared in chapter 5.

Species	Group sizes avg. range and (total range)	Adult female : Adult male sex ratio	Home Range (ha) variation	Path length (m) avg. variation and (total variation)
African Colobines				
Colobus angolensis	4.9-300+ (2-300)	1.6:1.3	371 – 2440	983 (312-1914)
C. guereza	5-19 (2-23)	2:1 - 3.3:3.1	2-100	386-609 (62-1360)
C. polykomos	11-16.2 (11-19)	4.7:1.2 - 4:3	24-77	618-832 (241-1410)
C. satanas	9-17 (7-25)	6:2.3 - 5:2	60-573	459-852 (20-1983)
C. vellerosus	14-16 (4-33)	6.5:3	9-48	300-359 (75-712)
Piliocolobus badius	25-52 (14-64)	18.3:10.5 – 10.8:2.1	20-58	872-967 (300-1532)

P. gordonorum	12-25 (5-34)	9.3:2.8	--	--
P. epieni	46 (15-80)	26:7	73	1040 (450-1900)
P. foai	12 (3-18)	--	--	--
P. kirkii	31-38 (20-65)	14.9:4.7 - 12:3.9	5-60	310-1044 (1-1270)
P. preussi	47 (24-80)	--	--	--
P. rufomitratus	11 (4-24)	5.6:1.1	9-13	461-603 (180-870)
P. tephrosceles	82	24:11	65-114	649 (223-1185)
P. tholloni	60	--	--	--
Procolobus verus	7-9 (2-14)	3.5:2 - 3:1.5	28-56	1212 (482-2105)
Asian Colobines				
Semnopithecus dussumieri	15-37 (1-54)	7.9:1 - 1.6:1	4-775	1083-1500 (583-1500)
S. schistaceus	18 (7-100)	2.6:1	1275	--
S. ajax	12-47 (7-100)	--	20-1200	--
Trachypithecus vetulus	--	3.4:1	2	--
T. johnii	8-17 (3-27)	1.2:1	6-260	--
T. auratus	14 (10-20)	6.5:1	2.5-8	--
T. cristatus	35 (10-35)	4.6:1	--	200+
T. obscurus	17	2.4:1	17-33	560
T. pileatus	8-10 (3-13)	3.3:1 - 3.6:1	14-64	324-800 (300-800)
T. geei	8 (4-22)	1.5:1 - 3.8:1	150-600	--
T. phayrei	--	--	30	--
Presbytis femoralis	11	4.8:1	22	935
P. siamensis	14-16	2.6:1 - 7.8:1	21-27	750
P. comate	8	3:1	14-40	500 (250-900)
P. thomasi	8	3:1	14	640 (150-1300)
P. hosei	7-10 (1-11)	--	35	740
P. rubicunda	6-7 (3-12)	2:1 - 2.6:1	33-99	850 (225-1670)
P. potenziani	3-4	1:1	33 (11.5-34)	540 (60-1120)
P. melalophos	6-15 (6-18)	--	14.5-29.5	614-717 (300-1360)
Simias concolor	4-5 (3-20)	1.7:1 - 1.8:1	3.5-20	--
Nasalis larvatus	9-17 (1-40)	3.6:1 - 7.5:1	130-900	315-910 (315-1810)
Rhinopithecus bieti	15 (15-269)	3.2:1 - 2.3:1	1100-5000	--
R. roxellana	12 (4-500)	1.6:1 - 2.7:1	1000-5500	710 (0-2870)
R. brelichi	6-15 (3-400)	2.2:1	610-3500	--
R. avunculus	14-20 (7-100)	1.8:1	--	--
Pygathrix nemaeus	9 (1-51)	1.9:1 – 2.7:1	--	--
P. cinerea	15 (2-88)	2:1	984	1080 (50-4080)
P. nigripes	7-13 (1-45)	1.8:1 - 2.1:1	42-47	514-1264 (514-1666)

2.8.2. Odd-nosed colobines

2.8.2.1. *Siamas, Nasalis,* and *Rhinopithecus*

Siamas concolor– Watanabe (1981) reported that *S. concolor* often live in monogamous pairs but groups can include up to 20 individuals. All-male units were also observed, and were observed more frequently in disturbed habitat possibly because of high hunting pressures in those areas.

Nasalis larvatus– Bennett & Sebastian (1988) and Yeager (1991) reported that *N. larvatus* lives in one-male units, the home ranges of units overlap completely, and units frequently fuse in the evening. Group sizes averaged between nine and 17 individuals. Both males and females dispersed, including observations of females with infants dispersing (Murai et al., 2007; Rajanathan & Bennett, 1990). Yeager & Kool (2000) reported juvenile females sometimes associate with all-male units. Males usually disperse before sexual maturity (Boonratana, 1994). Matsuda et al. (2009b) indicated little to no aggression between groups, suggesting this was related to the overlap of home ranges. Boonratana (2011) noted a lack of a birthing season.

Rhinopithecus bieti– Group sizes among *R. bieti* are extremely diverse, ranging from 15 (Kirkpatrick, 2011) to 269 individuals (Wu Baoqi, 1993), although the latter report is the fusion of multiple groups (referred to as a super-troop). Kirkpatrick (1998) indicated a 1:2 adult male to female ratio. Liang-Wei Cui et al. (2008) reported that groups consist of one-male units which fuse together, although there are some units that are multi-male/multi-female, monogamous or all-male (Kirkpatrick, 1998).

Rhinopithecus roxellana– Kirkpatrick (1998) reported group sizes of *R. roxellana* varied between 30 and 500 individuals (super-trooping). Sex ratio is about 1:2 adult males to females.

Bleisch & Jiahua Xie (1998) suggested a seasonal fission-fusion pattern related to food abundance and distribution, with increased fusion in the summer and increased fission in the winter. However, conflicting reports also suggested fission-fusion is related to reproduction and mating cycles (Kirkpatrick, 1998). Su Yanjie et al. (1998) reported all-male units (four to seven individuals) and one-male units (12 individuals) among *R. roxellana*, with super-troops ranging between 95 and 340 members. Ren Renmei et al. (1998) noted that all-male units remain along the periphery of super-troops.

Rhinopithecus brelichi– Bleisch et al. (1993) and Bleisch & Le Xuan Canh (1998) observed groups of *R. brelichi* between three and 10 individuals in one-male units. Groups fuse in super-troops of more than 400 individuals, and all-male units remain on the periphery of these super-troops. Bleisch & Jiahua Xie (1998) indicated the seasonal pattern of fission-fusion was related to food distribution and phenology with increased fusion in the summer and increased fission in the winter.

Rhinopithecus avunculus– Pham Nhat (1993c) reported group sizes of *R. avunculus* to range between seven and 25 individuals, and although Boonratana & Le Xuan Canh (1998) recorded larger group sizes (50 to 80 individuals) the average was 15 individuals. This is similar to Le Khac Quyet & Covert (2010) who reported average group sizes of 14 to 20 individuals, with groups of up to 100 individuals observed. Sex ratio is about 1:2 adult males to females. Studies indicate one-male units and all-male units (Boonratana & Le Xuan Canh, 1998), in addition to multi-male units (Kirkpartrick, 1998). Boonratana & Le Xuan Canh (1998) further noted that groups frequently travel together, indicating significant home range overlap and little aggression.

Kirkpatrick (1998) reported that females of all *Rhinopithecus* species (except *R. avunculus* in which data were lacking), display their sexual receptiveness with a crouch, similar to the doucs (see section 2.4.2). Thanh Hai Dong et al. (2011) reported this crouching behavior among *R. avunculus*. There are some reports suggesting that male *R. roxellana* actively care for infants: Ren Renmei et al. (1998) reported an adult male carrying an infant, and Kirkpatrick (1998) noted males protecting females with infants. Similar behavior has been reported among captive red-shanked doucs (Kirkpatrick, 1998).

2.8.2.2. *Pygathrix*

Pygathrix nemaeus– Lippold (1977; 1995; 1998) reported that *P. nemaeus* live in one-male units, multi-male units, all-male units or as solitary individuals. Lippold (1977) reported the average group size was nine individuals and groups occasionally fused. Solitary males and females were observed, although it was unclear if both sexes disperse or if it was the result of habitat disturbance. Pham Nhat (1993c) estimated group size to range between four and 27 individuals, and Ratajszczak et al. (1990) estimated group size to range between 20 and 30 individuals. Lippold (1998) reported group sizes among red-shanked doucs to reach 51 individuals and black-shanked doucs to reach up to 36 individuals at the same site (Kon Cha Rang Nature Reserve). Phiapalath (2009) reported that groups of red-shanked doucs in Laos ranged from three to 45 individuals. Phiapalath et al. (2011) from this same study reported the average group size was 25 individuals ranging between 17 and 45 individuals. Phiapalath & Suwanwaree (2010) reported two groups of 17 and 39 individuals which Phiapalath (2009) reported at 19 and 39 individuals. Phiapalath et al. (2011) reported groups fissioned during the dry season when high quality foods were less abundant, and fused during the wet season, when fruit is in abundance. Sex ratios of *P. nemaeus* in Lippold (1977; 1998) and Pham Nhat (1993c) were about 1:2.5 adult males:females. Phiapalath et al. (2011) reported a sex ratio about 1:2 adult males to females.

Lippold (1977) reported that grooming bouts were primarily between adult females, and could last up to an hour. Juveniles in captivity were observed to groom and carry infants indicting the significance of alloparental care (Lippold, 1977). Ruempler (1998) reported that adult males protect infants and pregnant females. Phiapalath & Suwanwaree (2010) reported male protective behaviors among red-shanked doucs similar to *Rhinopithecus*, as adult males were occasionally observed to chase sub-adult males from adult females with infants. Aggressive encounters never exceeded this chase behavior, and were not observed between adult males.

Pygathrix nigripes– Hoang Minh Duc (2007) reported the average group size among black-shanked doucs was 10 to 13 individuals, with observations of solitary individuals and groups up to 45 individuals. One-male units and multi-male units, were observed in high frequency with one-male units forming the core social unit. Fission and fusion were often observed between units. Group sizes did not differ significantly between habitat types. Sex ratio was 1:2 adult males:females. Rawson (2009) reported group sizes of black-shanked doucs at about seven individuals, ranging from one to 26. He also noted a sex ratio at 1:2 adult males:females. Groups consisted mostly of one-male units. Group sizes were significantly larger in the wet season than in the dry season, but not significantly different among habitat types.

Pygathrix cinerea- Ha Thang Long (2007) suggested group size of grey-shanked doucs were reduced by more than half due to hunting. Ha Thang Long (2009) reported that average group size is 15 individuals, ranging from two to 88 individuals. Sex ratio was 1:2 adult males:females. One-male units and multi-male units were observed frequently, and all-male units and solitary individuals were also observed. Multi-male units were noted to be the result of fusion among units. Fusion occurred more frequently when young leaves were abundant and fission increased when fruits were abundant.

2.9. Ranging patterns in colobines

2.9.1. General patterns

Colobines tend to have small home ranges and daily path lengths when compared to cercopithecines. Home ranges frequently have a core area which is most regularly occupied, and sometimes aggressively defended against conspecifics. African and Asian colobine home ranges are typically below 100 ha, and daily path lengths are generally less than 1000 m (Fashing, 2011; Kirkpatrick, 2011). Population density appears to affect home range size, with greater densities resulting in smaller home ranges (Fashing, 2011). Among the greatest influences on ranging behaviors are food availability, food quality, and precipitation. Additionally, polyspecific associations influence ranging among *Procolobus* and some populations of *Piliocolobus*.

Table 2.9 above provides an overview of colobine home range sizes and daily path lengths. Odd-nosed colobines are reviewed in greater detail below. For specific information on the other colobines outlined in Table 2.9 see Bennett (1986), Bishop (1979), Clutton-Brock (1975), Curtin (1980), Dasilva (1989), Davies (1984), Davies et al. (1988), Decker (1994), Dunbar (1987), Fashing (2011), Fashing et al. (2007b), Fimbel et al. (2001), Fleury & Gautier-Hion (1999), Fuentes (1994), Gatinot (1977), Grimes (2000), Gurmaya (1986), Hadi et al. (2012), Hladik (1977), Kirkpatrick (2011), Kool (1989), Korstjens (2001), Marsh (1981b), McKey & Waterman (1982), Newton (1987; 1992), Oates (1977; 1994), Olson (1986), Poirier (1970), Ripley (1970), Ruhiyat (1983), Sayers & Norconk (2008), Siex (2003), Stanford (1991), Starin (1991), Struhsaker (1975), Sugiyama (1976), Suprianta et al. (1986), Teichroeb & Sicotte (2009), Tenaza & Fuentes (1995), and Watanabe (1981).

2.9.2. Odd-nosed colobines

2.9.2.1. *Siamas, Nasalis,* and *Rhinopithecus*

Simias concolor– Watanabe (1981) reported that *S. concolor* had smaller home ranges in disturbed forests (3.5 ha) and larger ranges in undisturbed forests (30 ha). Similar results were observed by Tenaza & Fuentes (1995). Hadi et al. (2012) noted home ranges between four and 10 ha with minimal overlap between groups, although significant overlap with *P. potenziani* groups.

Nasalis larvatus– *N. larvatus* home ranges vary between 130 and 900 ha and daily path lengths average between 315 and 910 m (Bennett & Sebastian, 1988; Boonratana, 1994; Boonratana, 2000; Matsuda, 2008; Matsuda et al., 2009b; Salter et al., 1985; Yeager, 1989). However, Yeager (1989) reported a home range estimate as low as seven ha. Matsuda et al. (2009b) suggested differences in home range size are related to habitat, with smaller ranges among groups occupying mangrove forests and larger ranges among groups in mixed lowland forests. Group home ranges overlap significantly and groups often join each other, especially overnight. Matsuda et al. (2009b) observed home ranges contain a core area, but all intergroup encounters were non-aggressive even within the core area. Boonratana (2000) reported that daily path lengths increased when more young leaves were selected, but ranging was not correlated with availability of young leaves, phenology, or weather. Matsuda et al. (2009b) noted that daily path lengths significantly decease with increases in fruit availability.

Rhinopithecus species– Home range and daily path lengths of *Rhinopithecus* are the largest and longest in the colobine radiation. Long Yongcheng et al. (1994) reported home ranges among *R. bieti* as large as 4000 ha, and one report suggested 5000 ha (Kirkpatrick, 1998). The lowest home range estimate for this species was reported by Wu Baoqi et al. (1988) at 1100 ha.

These large home ranges are partly related to the seasonality of the environment, food scarcity and dispersal, and habitat disturbance (Qikun Zhao, 1988). Li Zhixiang et al. (1982) and Wu Baoqi (1993) observed that *R. bieti* occur at elevations between 3000 and 4300 m. Rui-Chang Quan et al. (2001) noted that *R. bieti* preferred higher elevations during the winter, and descended to lower elevations during warmer months. Bleisch & Jiahua Xie (1998) reported large home ranges (3500 ha) among *R. brelichi*. Schaller (1985) observed large home ranges (3000 ha) among *R. roxellana*, with the largest reported by Chen Fuguan et al. (1983) at 5500 ha. Su Yanjie et al. (1998) reported the home range of *R. roxellana* at 4000 ha, and daily path lengths from a few meters up to 2840 m, averaging 710 m. Of all non-human primates, *R. roxellana* live at the highest latitude, experience the longest winters and lowest temperatures, and they can descend over 1500 m from the summer to the winter foraging areas (Happel & Cheek, 1986; Schaller, 1985). Daily path lengths are between 500 and 2500 m (Hu, 1981). Pham Nhat (1993c) estimated home ranges among *R. avunculus* at 380 to 550 ha, and Boonratana & Le Xuan Canh (1998) estimated their home range at 1000 ha. Boonratana & Le Xuan Canh (1998) also noted that group ranges overlapped significantly, and groups often traveled, fed, and slept together, suggesting a high degree of fission-fusion behavior.

2.9.2.2. *Pygathrix*

Pygathrix nemaeus– Pham Nhat (1993c) estimated the home range of red-shanked doucs on Son Tra and other locales to be between 1500 and 3500 ha, although this was an estimate and high compared to quantified results. Phiapalath (2009) reported average home ranges among two groups to be 292 ha. He also noted seasonal variation in the usage of home range area, with the dry season at 253 ha and the wet season at 113 ha. The wet season was characterized by abundance in high quality foods, suggesting groups maintain a core area when high quality food is abundant and increase ranging when it is scarce.

Pygathrix nigripes– Hoang Minh Duc (2007) reported home ranges among black-shanked doucs at 42 to 47 ha with significant overlap in home range area between groups, and an average daily path length of 976 m. There were variations in the usage of home range area, which increased during the wet season along with high quality food abundance, and decreased during the dry season along with high quality food scarcity. Daily path lengths correlated negatively with precipitation, but did not differ between wet and dry seasons. Rawson (2009) reported the home range of black-shanked doucs was 20 ha, and estimated a daily path length of between 514 and 943 m, although this is not based on full-day follows.

Pygathrix cinerea– Ha Thang Long (2009) calculated home range for a group of grey-shanked doucs (88 individuals) at 984 ha. This group is possibly a super-troop, which may partly explain why the home range is much greater than found in other *Pygathrix* studies. Daily path lengths averaged 1068 m, ranging between 50 and 4080 m.

2.10. Activity budgets in colobines

2.10.1. General patterns

Among colobines there is assumed to be a greater need for resting, especially if diets are high in fiber. Resting usually follows feeding bouts to allow for long fermentation periods. In short, colobines are generally noted for their impressive coloration and relatively unimpressive activity patterns. Regardless, activity patterns are diverse between and within species, which in some instances relates to diet and/or habitat. Allogrooming tends to be the most observed social behavior.

Kool (1989) noted that there is bias involved when comparing activity patterns due to differences in methods between studies (definition and classification of activities and ages, visibility and use of scan or focal sampling), and different group compositions have different effects on activity. These concerns apply to all socioecological data. African colobine activity budgets have been studied more extensively than Asian colobine activity, and these studies provide interesting comparative materials because they explore the potential influence of feeding, seasonality, group composition, habitats, anthropogenic effects, and other behavioral aspects such as reproduction on activity patterns.

In general, reviews of Asian colobine activity patterns are absent from the literature. Table 2.10 provides a review of colobine activity patterns. Odd-nosed colobines are reviewed in greater detail below. For specific information on the other colobines outlined in Table 2.10 see Bocian (1997), Chengming Huang et al. (2003), Clutton-Brock (1975), Dasilva (1989), Fashing (2001a; 2011), Fashing et al. (2007b), Hadi et al. (2012), Marsh (1978; 1981c), McKey & Waterman (1982), Newton (1992), Oates (1977; 1994), Qihai Zhou et al. (2007), Sayers & Norconk (2008), Siex (2003), Struhsaker & Oates (1975), Teichroeb et al. (2003), Tenaza & Fuentes (1995), Werre (2000), Workman (2010a), Zhaoyuan Li (1992), and Zhaoyuan Li & Rogers (2004).

Table 2.10. Activity budgets of colobines. Based on above references. Data from this study are not included but compared in chapter 6.

Species	Percentage of time spent in activities				
	Rest	Feed	Move	Social	Other
African Colobines					
Colobus angolensis	32-43	27-42	20-24	5	1
C. guereza	52-63	19-26	2-22	5-11	1-7
C. polykomos	61	28	9	1	1
C. satanas	60	23	4	14	0
C. vellerosus	59	24	15	3	0
Piliocolobus badius	52-55	21-37	5-13	13	1-3
P. epieni	33	37	25	6	0
P. kirkii	44-47	29	6-12	7-15	5-7
P. rufomitratus	48-55	23-30	7-24	3-8	0
Procolobus verus	40	27	25	--	8
Asian Colobines					
Semnopithecus dussumieri	42	26	13	14	--
S. ajax/schistaceus	40	29	18	13	--
Trachypithecus delacouri	61	29	6	4	0
T. francoisi	52	23	17	8	
T. p. leucocephalus	50-74	13-17	11-18	18	
Presbytis potenziani	46-48	26-32	6-24	1-2	1
Simias concolor	50	28	6	2	2
Nasalis larvatus	76	20	4	1	--
Rhinopithecus bieti	33-35	35-39	10-15	13	16
R. roxellana	36	36	23	5	--
R. avunculus	23-32	15-~18	40-20	9-24	--
Pygathrix nemaeus	26-49	29-34	7-23	6-15	3-6
P. cinerea	37	12	26	25	0.1
P. nigripes	43-61	27-35	7-15	3-6	1-2

2.10.2. Odd-nosed colobines

2.10.2.1. *Siamas, Nasalis,* and *Rhinopithecus*

Simias and *Nasalis*– Hadi et al. (2012) reported the budget of *S. concolor* involved 50% resting, 28% feeding, 6% traveling, with social (2%) and other (2%) activities accounting for the remainder of the budget. Matsuda (2008) reported on the budgets of *N. larvatus*, with annual values highest for resting (77%), followed by feeding (20%) and moving (4%), with minimal social/other behaviors (1%).

Rhinopithecus species– Songtao Guo et al. (2007) observed *R. roxellana* rested (36%) and fed (36%) most often, followed by moving (23%) and social behaviors (5%). They reported increased moving and decreased feeding during summer months to exploit high quality and dispersed resources. The increased feeding and resting during the winter related to the exploitation of lichens and low quality food resources. Wei Ding & Qi-kun Zhao (2004) reported that *R. bieti* fed (35%) and rested (33%) most frequently, followed by moving (15%) and social activities (13%). During warmer months social activities increased and feeding and resting decreased. During winter months when more lichens were consumed, resting and feeding increased. Long Yongcheng et al. (1998) also examined activity patterns among *R. bieti*, reporting that feeding (39%) and resting (35%) were the most frequent activities, followed by moving (10%) and various social (grooming, display, play) and other activities (16%). Feeding peaked in morning and evening, and there were long periods of resting during the day. Kirkpatrick (1996) reported a relatively high percentage of grooming among *R. bieti* (8.4%). Boonratana & Le Xuan Canh (1998) reported similarly high grooming among *R. avunculus* (9.7%), although most of their time was spent traveling (40%) and as inactive or vigilant behavior (23%). Dong Thang Hai (2007) reported the activity budgets of *R. avunculus* involved a high amount of resting (33%), traveling (19%), and social activities including self-grooming (18%), followed by feeding (15%) and vigilance (15%).

2.10.2.2. *Pygathrix*

Pygathrix nemaeus– Lippold (1977) noted allogrooming was frequent among doucs in Son Tra. Otto (2005) reported on three male red-shanked doucs within a semi-wild enclosure over 10 days, and on these same three individuals in cages over a single day. In the semi-wild enclosure they rested (49%) most frequently, followed by feeding (34%), moving (7%), social (6%), and other activities (3%). In cages, their activity budgets were comparable; resting (51%), feeding (34%), moving (8%), and socializing (3%), with other activities (3%). Phiapalath (2009) reported adult red-shanked doucs from Laos feed most often (40%), followed by resting and inactivity (33%), traveling (10%), socializing (5%) and other activities (14%). “Other” activities in his study include self-grooming and play behaviors. Phiapalath & Suwanwaree (2010) reported annual activity budgets among all individuals from the same data set, noting that feeding was again most frequent (29.5%). Resting (12%) and inactive (14%) combined (26%) were also frequent, as was traveling (10%), and foraging/traveling in between feeding bouts (13%) when combined (23%). Social (15%) and other activities (6%) were reported, with the most frequent social activities being self-grooming and play. Despite the magnitude of differences in these results, they are from the same study groups. Phiapalath & Suwanwaree (2010) reported their study group which inhabited the more disturbed forest tended to rest less, and were more vigilant and traveled more compared to the other group during the dry season, which is when hunting was more frequent. Alternatively, Phiapalath & Suwanwaree (2010) suggested that food scarcity during the dry season accounted for increased travel time, and food abundance during the wet season accounted for increased feeding and resting time. Using only adults from the same data set Phiapalath (2009) illustrated that travel time did not change significantly between seasons.

Pygathrix nigripes– Hoang Minh Duc (2007) reported that resting (43%) and feeding (35%) were the most common activities among black-shanked doucs, followed by moving (15%), socializing (6%) and other activities (1%). In the dry season, resting and moving decreased and feeding increased, and this might relate to high quality food scarcity. In the wet season, feeding decreased and resting and moving increased, and this might relate to high quality food abundance. Allogrooming and male threat behaviors increased during the dry season, and play and intercourse increased in the wet season. Feeding peaks were in the morning and late afternoon with a significant resting peak during mid-day. Rawson (2009) reported inactivity (resting and vigilance) of black-shanked douc accounted for 61% of the time, followed by feeding (27%), traveling (7%), socializing (3%) and other behaviors (2%). Allogrooming behavior dominated social activities. Rawson (2009) reported a similar daily schedule as Hoang Minh Duc (2007). There were no differences between adult male and adult female activity budgets. The wet season was characterized by increased resting and decreased feeding, although these were not significantly different.

Pygathrix cinerea– Ha Thang Long (2009) and Ha Thang Long et al. (2010) reported the most common activity among grey-shanked doucs was resting (37%), followed by traveling (26%), socializing (25%), feeding (12%) and other (0.1%). Daily activity was similar to patterns described for black-shanked doucs. No significant differences were found between adult male and female activity budgets, although adult males tended to spend more time self-grooming than adult females, who generally spent more time resting and feeding. The wet season was characterized by decreased travel and feeding, and increased resting. The wet season is also when fruits and seeds were most abundant and selected.

Studies with the most robust data and methodology sets are found among the black-shanked and grey-shanked doucs, which thus provides the best comparable materials. Comparisons with activity budget studies on red-shanked doucs are done cautiously.

Chapter 3. Research site and methodology

3.1. Introduction

This chapter is divided into two sections: research site and methodology. The first section provides a detailed description of the study site including the topography, administrative structure, management, climate and weather data, forest types, biodiversity, and information on the red-shanked doucs at the site. This is followed by a description of the threats to biodiversity on Son Tra including the impacts of war, hunting, and development.

In the second section, the methods used in the study are described including the selection of Son Tra as a study site, the research approach, research equipment used, the habituation of the primary research group, behavioral observation methods, phenology transect establishment and monitoring, feeding tree measures and plant sampling, and chemical and nutritional analyses.

3.2. Research site

3.2.1. Location, topography, and biogeography

Son Tra Peninsula (Figure 3.1) is a rocky peninsula on the south-central coast of Vietnam located between 16°06’N to 16°09’N and 108°13’E to 108°21’E (Birdlife International Sourcebook, 2004; Lippold, 1977; Van Peenen et al., 1971), approximately 4,552 ha in size, and represents the easternmost portion of the Annamite uplift (Birdlife International Sourcebook, 2004). The peninsula borders the outskirts of Da Nang City, the fifth most populated city in Vietnam. Birdlife International Sourcebook (2004) reported Son Tra Peninsula was formed when alluvial deposition created a land bridge between the mainland and three small islands that now form the peninsula (Nghe, Mo Dieu, and Co Ngua). Mount Son Tra is the tallest mountain at 696 m. The waters surrounding the peninsula are shallow in areas (one to 10 m) out to around one km. Son Tra represents an isolated forest patch surrounded by Da Nang City and the South China Sea.

From the biogeographic perspective, an intriguing question is the length of time the forests on Son Tra Peninsula have been separated from other forests in the area, for example the forests on Hai Van Pass to the north. There is little geologic or specific biogeographic information on Son Tra, and the following review speculates on two alternative hypotheses.

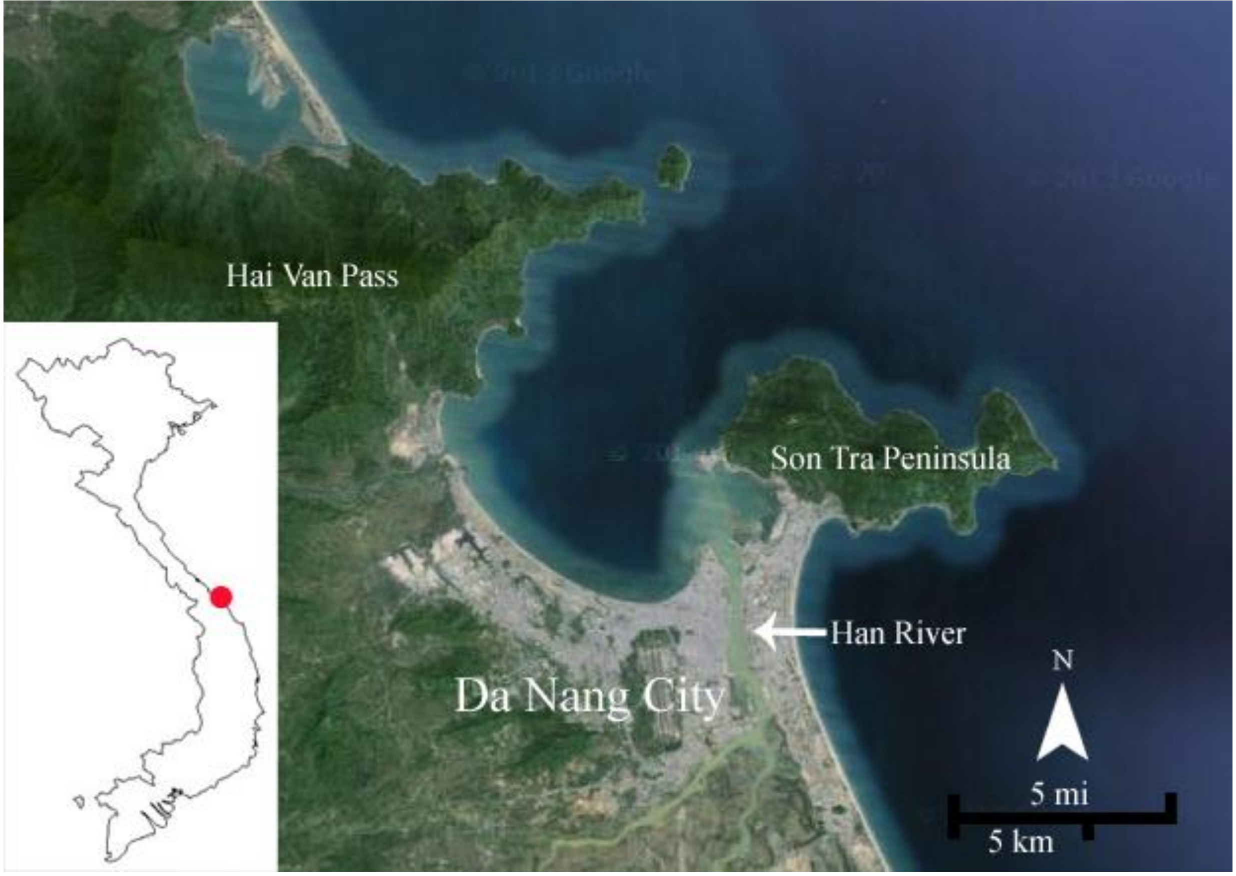
The Sunda shelf and low sea levels 18 kya allowed for a forested connection between current islands and the mainland (Jablonski, 1998; Liedigk et al., 2012; Roos et al., 2011; Sterling et al., 2006). There would have been a significant land connection between Hai Van and Son Tra and the doucs might have come to Son Tra at that time, though they would have had the opportunity to migrate from the north as recently as the late 19th and early 20th centuries.

Another hypothesis suggests that Han River changed course to its current position a few thousand years ago, having previously emptied south of Son Tra Peninsula (Tilo Nadler, 2010, personal communication). Presently, Han River empties into Da Nang Bay west of Son Tra Peninsula (see Figure 3.1). If the Han River emptied south of Son Tra, then Hai Van and Son Tra would have formed an uninterrupted forest block. Any wildlife migration, thus, would have been made even easier. According to Meijaard & Groves (2006), the Mekong River changed its southern course as recently as 5000 years ago, and Groves (2007a) noted changes in river courses are common as smaller tributaries form and gather the main flow. Loan Thi Kim Ho & Umitsu (2011) illustrated the Han and Thu Bon Rivers to the south of Da Nang are connected by several small tributaries, and were connected by larger tributaries in recent history, indicating that either river at one time flowed primarily into the other. Changes in the width and course of

Han River are likely to have occurred over the last few thousand years. Regardless, the duration that the forests on Son Tra have been isolated is unknown, although this is not likely to be long.

Van Peenen et al. (1971) found that several animals on Son Tra (*Tupaia glis modesta*, *Cynopterus sphinx*, *Leopoldamys sabanus revertens*, *Atherurus macrourus*, and *Paradoxurus hermaphrodites cochinensis*) have smaller body measurements and in some cases different fur colorations than conspecifics from elsewhere in Vietnam, suggesting that isolation has been at least long enough to result in variation among some taxa.

Figure 3.1. Map of Son Tra and Da Nang City.
(Google Earth, 2013)



3.2.2. Administrative structures and management

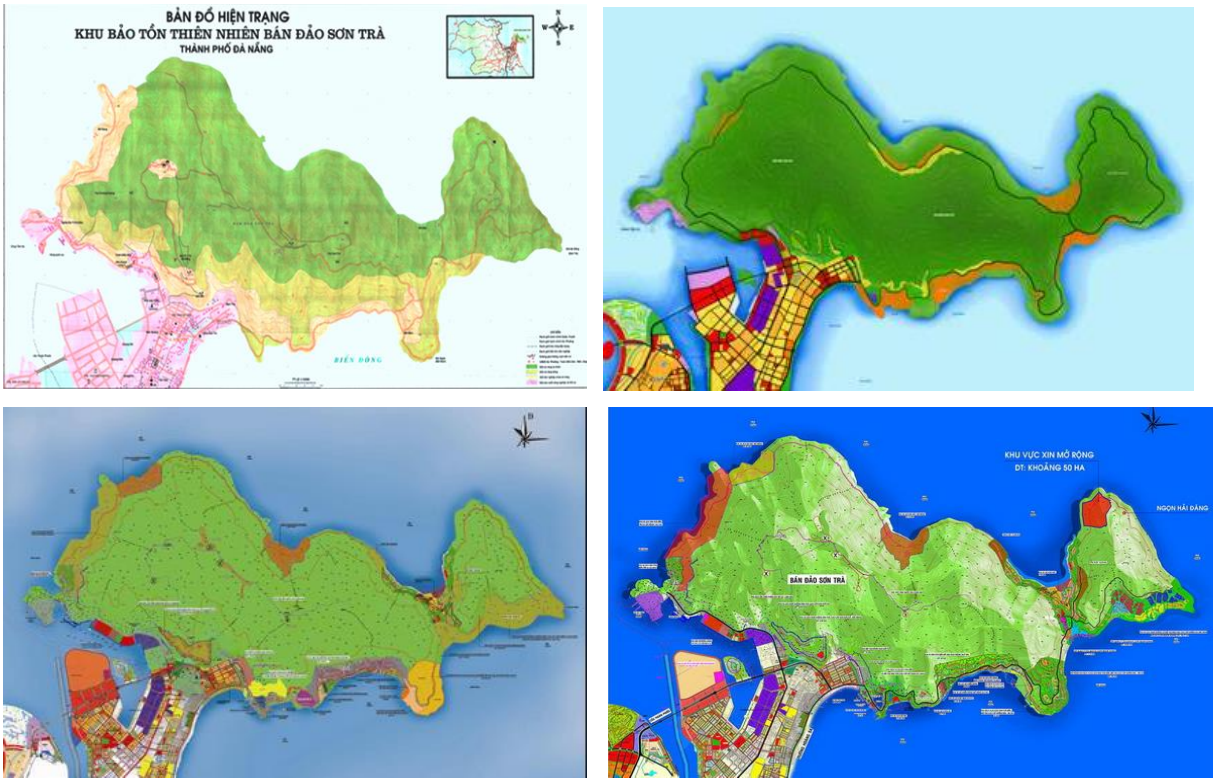
According to the Birdlife International Sourcebook (2004), Son Tra was established in 1977 as a 4,000 ha cultural and historical site by the Prime Minister, Decision No. 41/TTg, 24.01.1977. In 1989, the establishment of Son Tra Nature Reserve with a total area of 4,439 ha was proposed of which 2,595 ha were strictly protected forests and 1,844 ha were rehabilitation forest. Following approval of the proposal by the Quang Nam-Da Nang Provincial Peoples Committee and Ministry of Forestry in 1992, Son Tra Nature Reserve was officially established by Decree No. 447/LN-KL of the Prime Minister.

When the investment plan establishing the Nature Reserve was compiled, the area reportedly included 400 ha of primary forest and 2,611 ha of secondary forest. The area contains evergreen forests, plantation forests, grasslands and shrub, and agricultural lands (Birdlife International Sourcebook, 2004). The investment plan reported 4,189.7 ha of forested land within the reserve (Vu Ngoc Thanh et al., 2007), and the reserve covered most of the peninsula.

Son Tra Nature Reserve has been recently reduced to 2,670 ha and much of the previously protected land is now real estate land with several areas already under development by resort companies (Vietnam Conservation Fund, 2009). The exact boundaries of the Nature Reserve remain unclear and to date no map showing exact boundaries has been made available by city administration. Therefore, the map in Figure 3.2 shows the estimated boundaries based on personal observations and communications with Nature Reserve staff. Boundary lines tend to follow the new coastal road around the peninsula, which was completed in 2012. Figure 3.3 shows maps from the Da Nang City Government website collected over the past four years (Da Nang Government, 2012). These maps illustrate locations of current and planned development and show that areas previously included in the reserve are now open for development. In these maps, the green areas represent forest, not the Nature Reserve boundaries.

Figure 3.2. Approximate boundaries of Son Tra Nature Reserve in green.
(Google Earth, 2013)

Figure 3.3. Maps of Son Tra by Da Nang City Government (2012). Green areas represent forests, not Nature Reserve boundaries.



3.2.3. Forests on Son Tra

The forests on Son Tra contain members of 143 plant families (Birdlife International Sourcebook, 2004; Dinh Thi Phuong Anh, 1997).

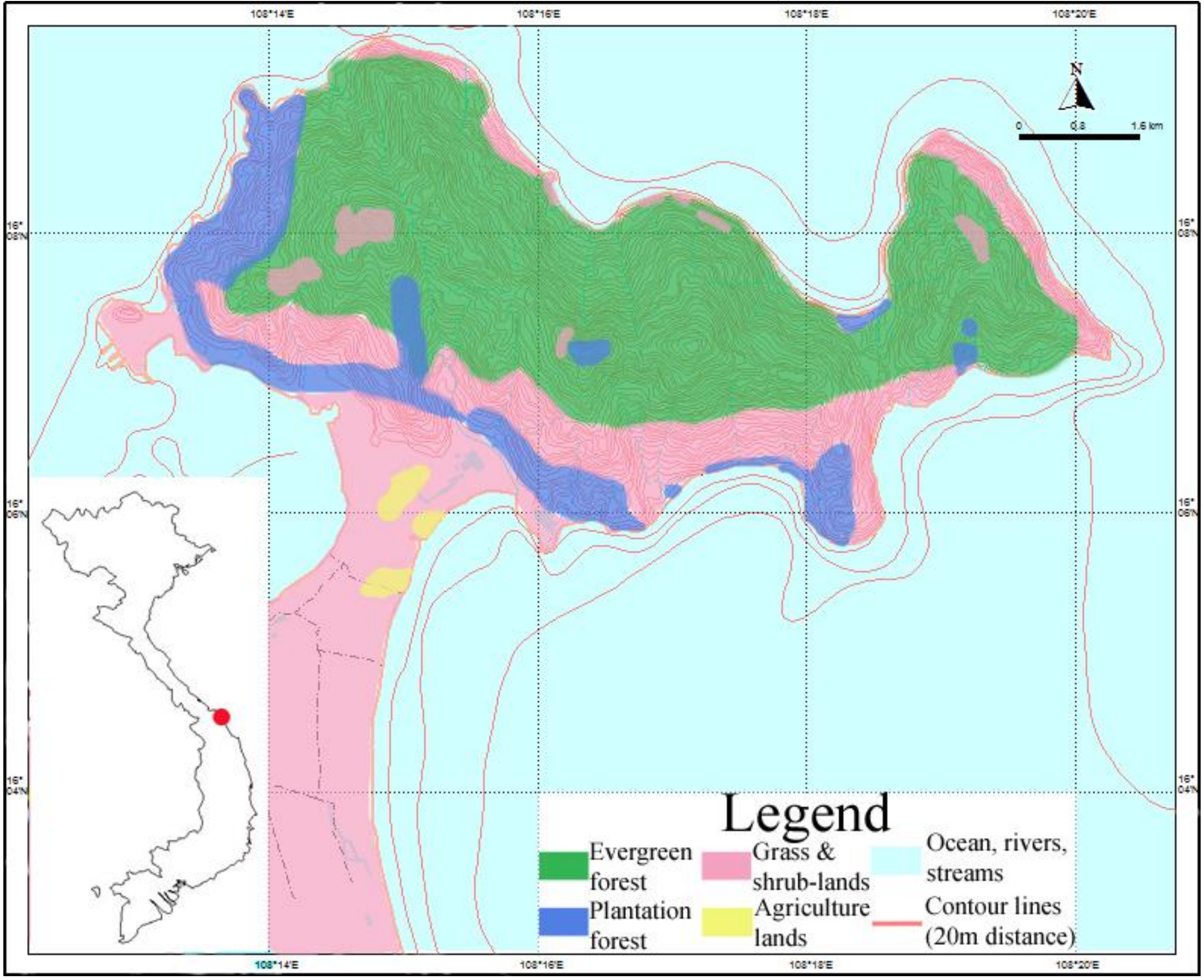
The first detailed classification of Son Tra's forest was made by Van Peenen et al. (1971). They reported that Son Tra differed from the often described deciduous forests of Indochina, noting that the majority of trees do not shed leaves and those that do shed leaves do so at different times of the year rather than in seasonal concert. They also noted higher elevations on Son Tra are often covered in clouds throughout the year and received more rain than lower elevations. They classified Son Tra forests under five forest types: tropical primary forest, secondary moist forest, secondary dry forest, grasslands, and cultivated lands. Tropical primary rain forest occurred in patches on the northern slopes above 300 m with trees reaching 40 m height, contained a second younger tree canopy, sparse undergrowth full of vines and epiphytes, and corresponds with rain forest criteria established by Williams (1965). Secondary moist forest occurred mostly above 300 m where many tall trees have been cut, trees reached 15 m height although scattered taller trees were present, the undergrowth was dense forming many different ecotopes of vines, shrubs, thorny palms and bamboo, with a mix of deciduous and broadleaf evergreen trees. It was noted that this was primary rain forest but due to disturbance it was classified as moist mixed deciduous forests according to Williams (1965). Secondary dry forests were found on south slopes at lower elevations and mainly consist of shrubs and vines with shorter trees, corresponding to moist mixed deciduous forests by Williams (1965). Grasslands on Son Tra occurred as a result of annual clearings. Cultivated lands occurred on parts of the south slope.

Lippold (1977) reported the same five forest types but Dinh Thi Phuong Anh et al. (2010) distinguished only three forest types: a) tropical moist evergreen broad-leaf forests, b) dry secondary forests, and c) scrub and grass-lands.

Van Peenen et al. (1971) and Lippold (1977) noted the forests on the southern parts of Son Tra were heavily disturbed and even cleared by the United States military in some areas. Personal observations confirmed heavy disturbance in this area but also in section of the eastern and western parts of the peninsula. However, the northern part is largely undisturbed aside from the coastal road and ridge road. Most of this area contains good quality secondary forest similar to the descriptions in Van Peenen et al. (1971), including tropical primary forest with patches containing numerous tall (40 m) and wide (30 m) trees, a healthy secondary canopy, and undergrowth with many vines. Mangrove forests were previously reported (Lippold and Vu Ngoc Thanh, 2008), but no longer occur on Son Tra.

In general, Van Peenen et al.'s (1971) forest classification for Son Tra remains accurate and relevant. The map in Figure 3.4 shows the different forest types as reported in Birdlife International Sourcebook (2004).

Figure 3.4. Forest types on Son Tra.
Adapted from Birdlife International Sourcebook (2004), Lippold and Vu Ngoc Thanh (2008).



3.2.4. Weather patterns and climate

Under the Köppen (or Köppen-Geiger) climate classification (see Köppen & Geiger, 1936; Peel et al., 2007), the north-central Annamites are located in the Tropical Monsoon Climate belt and the southern Annamites are located in the Tropical Savanna Climate belt. The difference between the two is the former has a driest month with less than 60 mm precipitation and *more* than (100-[total annual precipitation (mm)/25]), but the latter has a pronounced dry season with the driest month having precipitation less than 60 mm and *less* than (100-[total annual precipitation (mm)/25]). Da Nang City is located geographically at the border between these two climates belts.

Four sources of weather data were used to assess the climate in Da Nang and Son Tra. First, weather data were obtained from Da Nang Hydrometeorological Center (2012) for the study period. Second, daily weather data from Da Nang City were also gathered from Wunderground (2013) with their permission. Third, data from Weatherbase (2013) provided averages over the last 20 to 50 years, and is used with their permission. Last, information gathered by Van Peenen et al. (1971) was reviewed.

According to these sources, Da Nang is most appropriately a southern classification with an annual precipitation of 1797.75 mm (2393.06 mm on Son Tra Peninsula). Köppen-Geiger further suggested tropical wet season months contained more than 60 mm precipitation. Based on precipitation data from the four sources, Da Nang has a tropical rainy season from June through January and a four month dry season from February through May. This is generally in accord with personal observations. This seasonal pattern is used as a basis throughout the dissertation.

There are differences in the weather between Da Nang and Son Tra. Data from Da Nang Hydrometeorological Center (2012) and data compiled by Van Peenen et al. (1971) are collected on Son Tra Peninsula at the lighthouse weather station on the northeastern coastline. Wunderground (2013) and Weatherbase (2013) present data collected from Da Nang International Airport in the heart of Da Nang City. To quantify the differences, this study compared daily temperature and precipitation data between Da Nang International Airport (Wunderground, 2013) and Son Tra lighthouse (Da Nang Hydrometeorological Center, 2012) over 2010 and 2011. Averages for these two years are presented in Table 3.1. This shows that Son Tra received more rainfall than Da Nang City during every month except February and

April. In November, at the peak of the raining season Son Tra received over 200 mm more rainfall than Da Nang City. The precipitation difference is statistically significant in a two-tailed paired *t*-test (*t*-test (729) = 4.545, p = 6.444E-06). Comparing each month individually, paired *t*-tests were significantly different for March, October and November. Precipitation trends are illustrated in Figure 3.5.

Similarly, temperature differed between Da Nang City and Son Tra, as shown in Table 3.2. Figure 3.6 illustrates temperature trends, showing that temperatures are typically cooler on Son Tra Peninsula. This difference is also statistically significant (*t*-test (729) = 11.75, p = 3.006E-29).

Even in dry season months, there were clouds with mist or light rain around the peaks of Son Tra above 300 m. In both seasons, there were often days when it did not rain in Da Nang City but rained on Son Tra above 300 m, where it was noticeably cooler. Therefore, the data presented here underestimates the amount of rain for higher elevations on Son Tra.

Figure 3.5. Precipitation data.
2010 & 2011 from Da Nang City International Airport (Wunderground, 2013), Son Tra Lighthouse (Da Nang Hydrometeorological Center, 2012), and Da Nang City Airport over the last 50 years (Weatherbase, 2013).

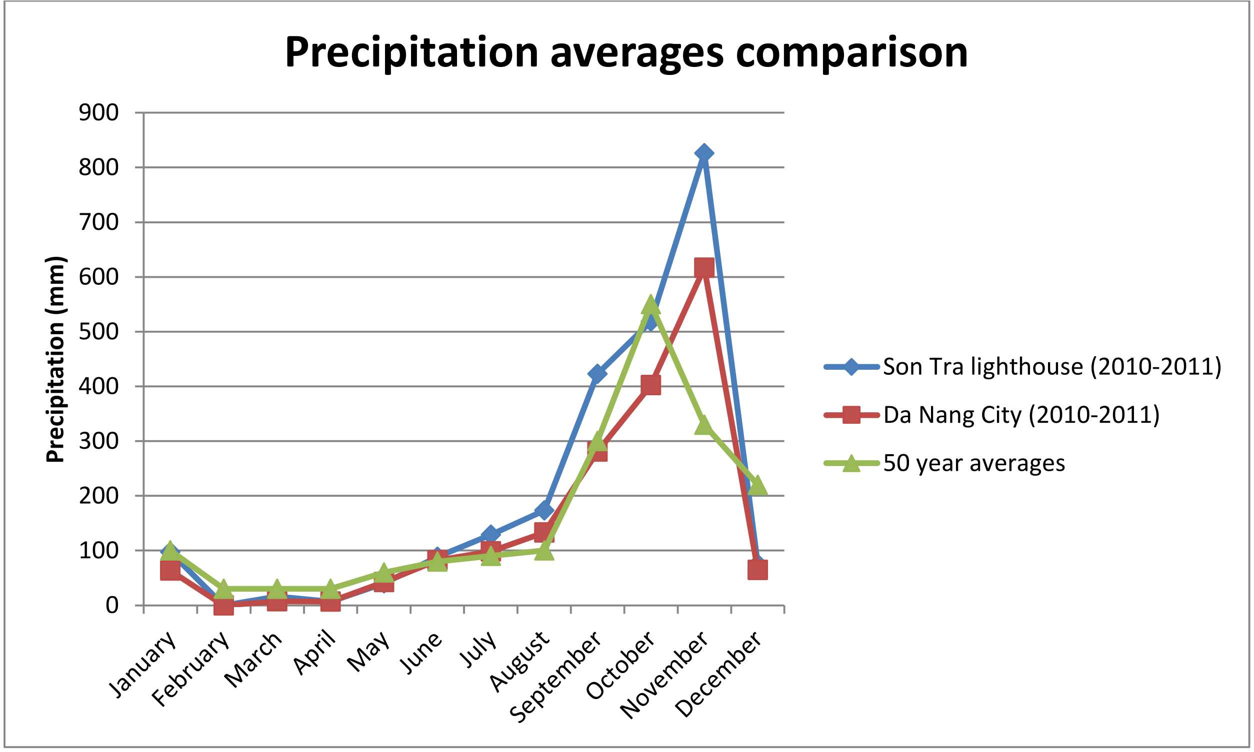


Figure 3.6. Temperature data.
2010 & 2011 from Da Nang City International Airport (Wunderground, 2013), Son Tra Lighthouse (Da Nang Hydrometeorological Center, 2012), and Da Nang City Airport over the last 20 years (Weatherbase, 2013).

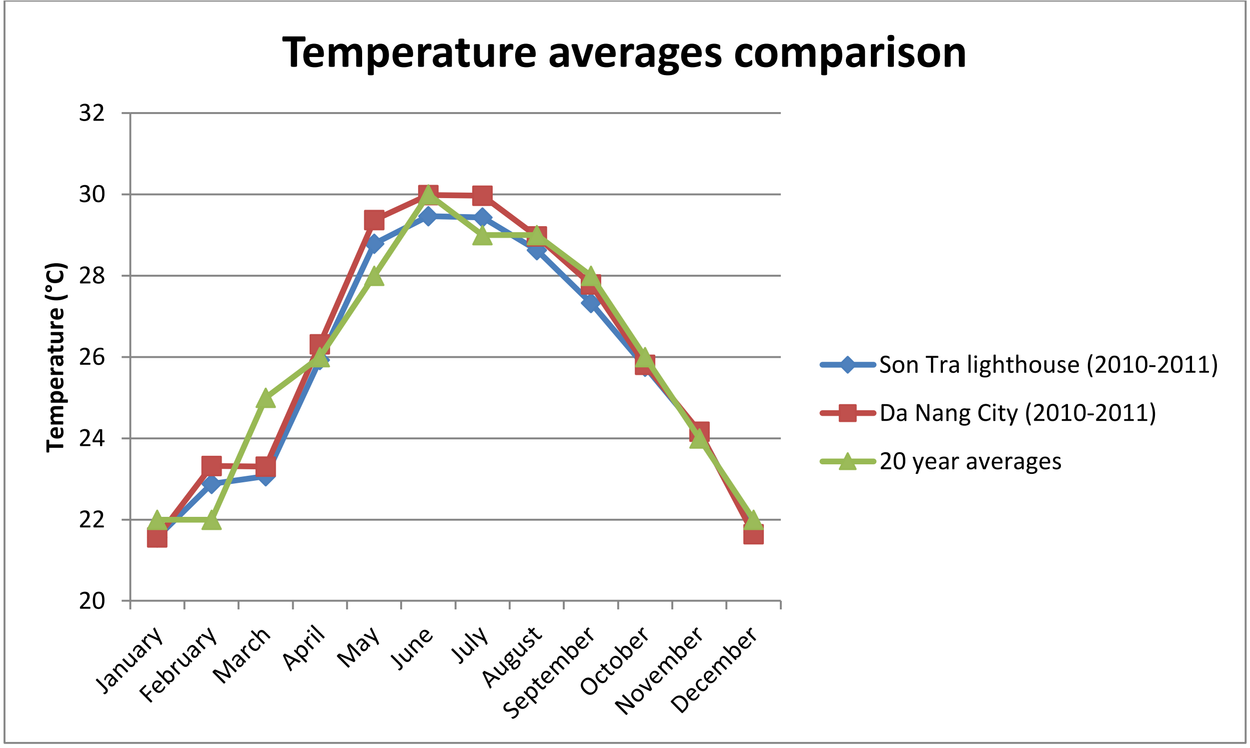


Table 3.1. Annual monthly precipitation, mm.

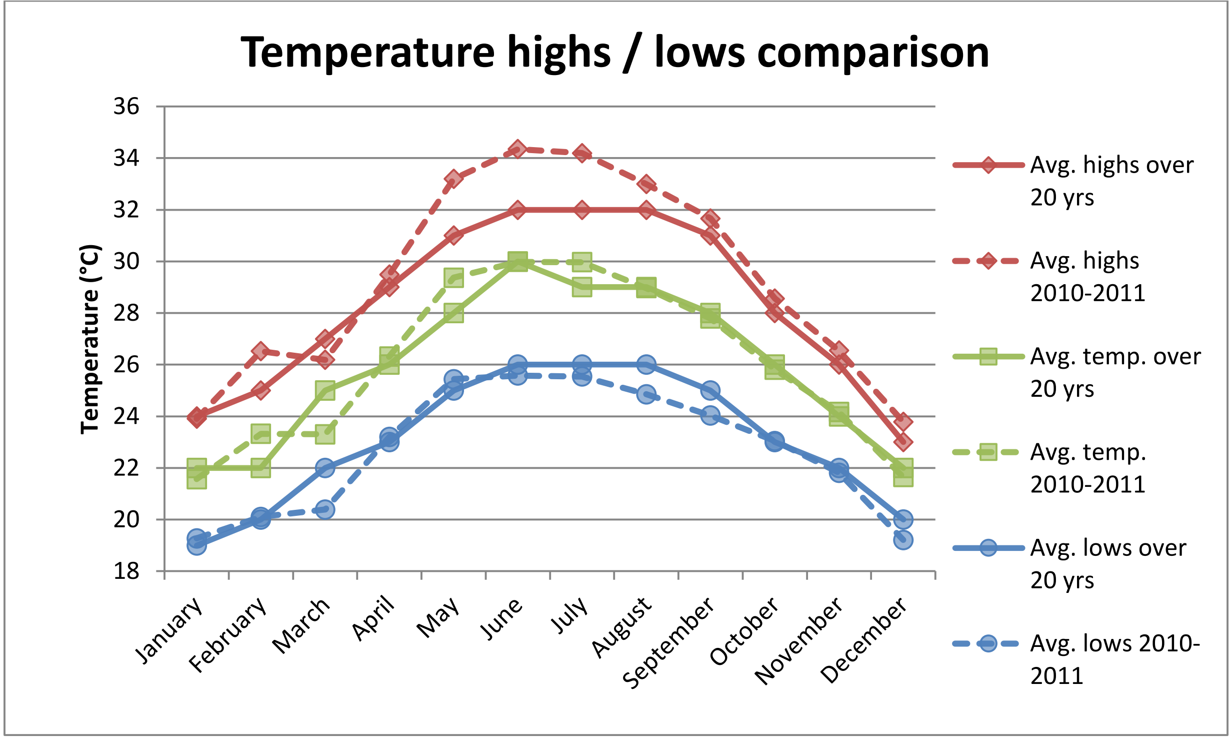
	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Son Tra Lighthouse (2010 & 2011)	97.4	0	15.8	6.45	40.2	88.3	129	173	423	519	826	75.0
Da Nang International Airport (2010 & 2011)	63.2	0	7.6	6.5	42.2	82.2	98.5	133	281	403	617	64.4
Da Nang Airport (last 20 years)	100	30	30	30	60	80	90	100	300	550	330	220

Table 3.2. Annual monthly temperature, degrees Celsius.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Son Tra Lighthouse (2010 & 2011)	21.6	22.9	23.1	25.9	28.8	29.5	29.4	28.6	27.3	25.8	24.2	21.7
Da Nang International Airport (2010 & 2011)	21.6	23.3	23.3	26.3	29.4	29.9	29.9	29.0	27.8	25.8	24.2	21.7
Da Nang Airport (last 20 years)	22	22	25	26	28	30	29	29	28	26	24	22

Finally, weather data during the study period were compared to annual averages, as illustrated in Figures 3.5, 3.6 and 3.7, and the above Table 3.1 and 3.2. As is seen, precipitation and temperatures during the study period did not differ from the averages recorded over recent decades.

Figure 3.7. Temperature: average lows and average highs.



3.2.5. Biodiversity

Biodiversity was first comprehensively recorded in 1997 by Da Nang University (Dinh Thi Phuong Anh, 1997). They reported 985 plants of 483 genera within 143 families, 36 mammal species of 18 families and eight orders, 106 bird species of 34 families and 15 orders, 23 reptiles of 12 families and two orders, nine amphibians of four families and one order, 113 insects of 26 families and 12 orders, and amongst them numerous threatened taxa. Considering the relatively small size of the area and its location this is a fairly high degree of biodiversity. During this study, I collected several specimens and photographed species that were not previously reported in the nature reserve. Combining these observations with those made by Van Peenen et al. (1971), Lippold (1977), Dinh Thi Phuong Anh (1997) and Vu Ngoc Thanh et al. (2007), Son Tra now currently contains one species of freshwater fish, two crustaceans (one freshwater shrimp and one crab), at least 142 insect species, 14 amphibians, 41 reptiles, 127 birds, 46 mammals, and at least 1022 plant species. This species list is provided in Appendices 1 through 6, and each are unlikely to be complete with entire phyla of common plants and orders of common animals not yet surveyed on Son Tra. For example, insect diversity is little studied on Son Tra and many reported insects remain unidentified. Also, nothing has been reported about the stream life which was first documented during this study including a freshwater fish and crustaceans found at nearly all elevations on Son Tra. However, I also believe several of the species that were confirmed in 1971 and 1997 may now be extinct locally.

Among the primates, Son Tra unquestionably contains rhesus macaques (*Macaca mulatta*) and red-shanked doucs. The population number of rhesus macaques on the peninsula has not been assessed, but based on my personal observations and encounter frequency, I estimate there are about twice as many macaques as there are doucs. Vu Ngoc Thanh et al. (2007) noted there may be pygmy loris (*Nycticebus pygmaeus*) on Son Tra, although this is based on a single captive loris presented to them at the ranger station. Lorises were not observed during this research, although one hunter did show me photographs of a trapped loris which he claimed had come from Son Tra within the year. Vu Ngoc Thanh et al. (2007) also confirmed stump-tailed macaques (*Macaca arctoides*) on Son Tra in interviews and through observations, although they noted that the species was rare. During my research no troop of stump-tailed macaques was observed, although one individual resembling a stump-tailed macaque was seen traveling with a troop of rhesus macaques. This may have been a stump-tailed macaque or a hybrid. Regardless, if stump-tailed macaques remain on Son Tra, they are very rare.

Another primate recorded by Lippold (1977) were gibbons, and she based this record on morning vocalizations in 1974. It cannot be known if these were captive gibbons, released gibbons or native wild gibbons, or how many gibbons they represent. Regardless, they are now extirpated. One plant collector on Son Tra reported observing an all-white douc, which could be a female gibbon traveling with the doucs. The FPD released two yellow-cheeked gibbons (*Nomascus gabriellae*) into Son Tra in 2006 (Education for Nature Vietnam, 2006). If the reported douc was a gibbon, it was most likely one of these released animals. Van Peenen et al. (1971) reported long-tailed macaques (*Macaca fascicularis*) were common at lower elevations and they collected two specimens. Long-tailed macaques were also reported by Lippold (1977) but were not reported by Dinh Thi Phuong Anh (1997), Vu Ngoc Thanh et al. (2007) or observed personally during this study, suggesting they are now extirpated.

3.2.6. Red-shanked doucs on Son Tra

The first report of red-shanked doucs on Son Tra was made in 1812 when a ship of unspecified origin docked at Da Nang Bay and the crew shot over 100 doucs between 5:00 am and breakfast (Sterling et al., 2006: 227). The next report was published in 1969 based on information gathered between 1966 and 1969 during the Vietnam-American War (Van Peenen, 1969), followed by a detailed report of Son Tra and its mammalian biodiversity by Van Peenen et al. (1971). A field study on Son Tra in 1974 gathered the first data on red-shanked doucs in the wild (Lippold, 1977). These studies did not venture a population estimate for doucs on Son Tra, but Lippold (1977) reported on three groups from four camp sites totaling 28 individuals. A decade later, MacKinnon & MacKinnon (1987) suggested the population on Son Tra was extirpated. A survey conducted in 1988 reported two groups of seven and 10 individuals remaining in the area (reported in Nadler et al., 2003). However, soon after Pham Nhat (1993b) cited a source (Do Tuoc, 1989) that suggested Son Tra contained 300 individuals. This citation was not referenced in Pham Nhat (1993b), has not been cited in any later publications, and has not been successfully located. A survey in 1995 reported 30 to 40 individuals on the peninsula

(Lippold, 1995), and Lippold (1998) noted the population of doucs on Son Tra was not extirpated but did not exceed 300 individuals. The presence of red-shanked doucs was confirmed in the following reports (Dinh Tri Phuong Anh, 1997; Dinh Thi Phuong Anh & Huynh Ngoc Tao, 2000), who estimated the population at 30 to 40 individuals. Nadler et al. (2003) shortly after these studies suggested that the population of doucs at Son Tra was very small if not extirpated.

In December of 2006, a survey by researchers from Da Nang and Ha Noi universities recorded 171 individuals in Son Tra, with a population estimate of 198 red-shanked doucs within 12 groups (Vu Ngoc Thanh et al., 2007). This meant it was one of the largest populations of red-shanked doucs in Vietnam and remains thus today. Lippold & Vu Ngoc Thanh (2008) suggested that nearly 60% of the red-shanked douc population in Vietnam may be located in Son Tra, implicitly indicating the population in Vietnam to be less than 400 individuals, although they provided no population data from any area to support their claim. Haus et al. (2009) conducted intensive field work in Phong Nha-Khe Bang National Park and estimated the red-shanked douc population was between 445 to 2137 individuals. This would make the Phong Nha-Khe Bang population the largest in Vietnam. Therefore, Son Tra contains the second largest known population in Vietnam, the only counted population as opposed to estimated, and between 10% and 30% of the total Vietnamese population. The most recent survey on Son Tra reported between 198 to 208 individuals of 13 groups (Dinh Thi Phuong Anh et al., 2010), which is in strong agreement with the observations made by Vu Ngoc Thanh et al. (2007).

As noted above, Sterling et al. (2006) reported the killing of more than 100 doucs during a morning in 1812, which suggests that doucs were more abundant on Son Tra at that time. This report together with that by Van Peenen et al. (1971) has a few implications for Son Tra’s douc population: a) the density of doucs during times with the forest was undisturbed or less disturbed must have been relatively high, b) there has been a major decline in the douc population, and c) red-shanked doucs on Son Tra may then have been traveling in super-troops similar to other odd-nosed primates.

3.2.7. Threats

3.2.7.1. Hunting and plant collection

Hunting on Son Tra has been highlighted as a main threat to the doucs and other wildlife as early as 1974 (Lippold, 1977; Lippold & Vu Ngoc Thanh, 2008; Thanh Nien, 2013; Vu Ngoc Thanh et al., 2007). I have observed numerous lines of snares numbering in the hundreds in several parts of the reserve. Both local people and military personnel were reported to hunt on Son Tra (Lippold & Vu Ngoc Thanh, 2008; Vu Ngoc Thanh et al., 2007). Doucs were also historically used for target practice by both the American and Vietnamese forces, but today the military does not appear to be involved in hunting (Lippold & Vu Ngoc Thanh, 2008). Logging and collection of fuel wood and non-timber forest products including resins, palm leaves, lantana, cycad leaves, and rattan further degrades Son Tra's habitats and has been reported to occur despite regular patrolling by military and forest protection personnel (Lippold 1977; Lippold & Vu Ngoc Thanh, 2008; Dinh Thi Phuong Anh et al., 2010; Vu Ngoc Thanh et al., 2007; Van Peenen et al., 1971). Resin collection focuses on dipterocarp trees, including important feeding trees for the doucs, and is a serious threat on Son Tra because collection involves the cutting of large holes into the trunk which weakens the structure of the tree over time and results in its collapse (Lippold & Vu Ngoc Thanh, 2008). Resins are collected and sold for use in boats as sealant and caulk (Le Phuoc Bay, 2007, personal communication; Lippold & Vu Ngoc Thanh, 2008; Pham Duc Chien et al., 2008).

3.2.7.2. War and development

War and development are two forces that have been critical to Son Tra and the survival of the doucs, and these forces continue to impact the peninsula.

In 2001, Prime Minister Phan Van Khai approved the *Overall Plan for the Socio-Economic Development of Da Nang City in the Period between 2001 and 2010* (Decision No. 113, 2001, QD-TTg, 21.03.2001). The primary goal of this plan was to develop Da Nang City into a major economic hub. The plan also stated, “Da Nang is one of the geographical areas holding an important strategic position in national defense and security for Southern Central Vietnam, the Central Highlands, and the whole country” (Decision No. 113, 2001, QD-TTg, pg.1). The following provides a historical perspective for the strategic significance of Da Nang and Son Tra Peninsula.

Da Nang was the main harbor for the French in central Vietnam, remains the only large harbor in central Vietnam, and is currently a main base for Vietnamese naval and marine forces. Son Tra was home to an American military base during the American-Vietnamese war. Van Peenen et al. (1971) noted that the main bases on Son Tra were for radar, observation and naval purposes. During the American occupation, several roads were built on the peninsula, and parts of the southern slopes were cleared. Although there are reports of dioxin contamination in and around Da Nang City (see An Dien & Dillingham, 2012; Sasaki, 2012), there are no reports of defoliates being used on Son Tra (Stellman et al., 2003). Due to the military presence on Son Tra, access to Son Tra was restricted until around 2007 when resort and tourist road construction were well underway. Lands owned, maintained or protected by militaries around the world are often linked to high biodiversity values (Boice, 2006; Henk, 2006; Jianguo Liu et al., 2003;

Ripley & Leslie, 1997; Stein et al., 2008; Warren et al., 2007), and the military control of Son Tra is almost certainly the reason why doucs survived there until today.

Son Tra is directly adjacent to Da Nang City, which is the fifth most populous city in Vietnam and the largest city on the central coast with 887,069 people (U.S. Bureau of East Asian and Pacific Affairs, 2010). Da Nang is also home to the third largest port in Vietnam (Da Nang Port, 2012). Given all of this, it can be assumed that the military presence is the only reason this remnant coastal forest patch has remained intact. Since 2007, military restrictions at Son Tra are relaxing, and at the same time development activities increase. The size of the protected area was recently reduced by nearly half to account for resort development, and recently the coastal road has been completed. Lippold & Vu Ngoc Thanh (2008) highlighted the impacts that roads and development are having on the peninsula, as resorts and roads begin to fragment the forest into ever smaller blocks. Nguyen Thi Tuong Vi et al. (2010) noted the declining biodiversity on Son Tra, and attributed this to the increasing development and decreasing military control.

The Overall Plan for Socio-Economic Development (Decision No. 113, 2001, QD-TTg) outlined the protection and restoration of the natural forests at Son Tra, including the planting of trees to protect against forest loss. The construction of a coastal road was also approved, which has caused considerable damage to biodiversity. The development of tourism on Son Tra is another focus, and Nguyen Thi Tuong Vi et al. (2010) noted this has proceeded with little regard to biodiversity. There are currently five resorts operating on Son Tra and five more in various states of development. All tourism activities have had direct and indirect impacts to the biodiversity and ecosystem of Son Tra similar to those discussed at the global scale by Strier (2011), including disturbance of habitat, littering, and an increased demand for wildlife products and non-timber forestry products.

3.3. Methods

3.3.1. Study site selection

When Son Tra was selected as the study site in 2007, it was the only site known where red-shanked doucs could be observed reliably in the wild. Reports of douc populations at all other sites suggested low numbers and usually significant hunting pressure. Son Tra Peninsula is relatively small, guarded partially by the military and was believed at the time to be home of the largest known population of red-shanked doucs in Vietnam. In addition, the well-established Frankfurt Zoological Society in Vietnam and Da Nang University indicated their willingness to cooperate and assist in obtaining research permits.

In 2007, I conducted a brief preliminary study on Son Tra with the assistance of Professor Herbert Covert, Le Khac Quyet, Dr. Dinh Tri Phuong Anh, and forest protection staff. The purpose of the study was to assess the feasibility of long-term research. Each day included several observations of doucs, cataloguing of food items, and assessing human impacts. This also permitted me to have direct observations of the hunting and development pressures on Son Tra. It became clear that unless conservation activities focus on Son Tra, there will be no doucs or other wildlife left in the foreseeable future. For me, this was motivation enough to persist in my endeavors to obtain a research permit despite numerous difficulties. Additional preparations for this research on Son Tra involved three months at the Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park just prior to research in order to practice identifying sexes and relative ages.

3.3.2. Observation methods

Initially, surveys in Son Tra were unsystematic and covered the entire peninsula. After the primary research group was selected, observations focused on this group although regular observations were made with several other groups/units, especially on days when the primary observation group could not be found. This group was chosen based on a fortuitous encounter that provided me with some knowledge of their home range (described below). During the course of research, it became easier to locate the primary research group with increasing knowledge of their home range and their increasing comfort around me.

Sleeping in the forest was not permitted by the Forest Protection authorities, which meant the forest had to be entered and exited each day. Research typically started between 5:00 and 6:00 depending on sunrise and ended between 17:00 and 18:00 depending on sunset. Research activities also finished earlier when contact with the primary observation group was lost and none of the other groups could be found. For several weeks, it ended earlier because confiscated doucs were being kept at the Son Tra ranger station, which meant the need to collect leaves and fruits for feeding in the evening and the following morning, seemingly a task of which the rangers were not aware or prepared for. This additional work gave me the opportunity to test and identify douc food sources correctly. Most of the confiscated doucs were released back into Son Tra, although one very badly injured douc was transferred to the EPRC, and one infant was transferred to the zoo in Ho Chi Minh City.

When entering the home range of the primary research group, I moved slowly and quietly until the doucs were heard (their movements or vocalizations). Doucs were almost always heard before they were seen. As I become more confident in finding the primary research group, I used a specific call constantly in and near their home range to alert them of my presence, so they could hear me coming before I was near. This may have initially resulted in the doucs hiding or moving away silently but had the positive effect that the doucs were never surprised by an encounter, which I wanted to avoid for the sake of observation and habituation. In the long term, I believe these vocalizations comforted the doucs to me as they always knew where I was without having to see me. On days with strong wind, heavy rain, or both, it was not possible to hear the doucs moving or calling. Unless the doucs had been followed to their sleeping site the previous evening, these days typically had no sightings of the primary group.

When following the doucs a distance of at least 30 m was maintained because closer distance resulted in threats and displays from group members directed to me or group members fleeing. Furthermore, at closer range it was very difficult to assess if other units or groups were nearby. During research, the rule was never to disturb the doucs and never to chase them, and this rule had precedence over observation. If following the doucs appeared to be agitating them, then observations ceased for the day. Disease transmission to the doucs was of little concern as I was never closer to them than 5 m, and all human waste was buried and rubbish removed.

Daily path length GPS marks were taken between movements exceeding 30 to 50 m. GPS marks were taken at the location of a focal individual as opposed to an estimated group center. This is because units and groups often dispersed in various directions, or dispersed quietly and unnoticed with the exception of one or two individuals. Despite the primary research group becoming increasingly habituated, full-day follows were rare. A full-day follow is a day which began with observations of the group waking up until they slept in the evening and was always verified by the presence of the group in the same trees at the start of the following day. Only if their presence the following morning was verified were the data used in path length analysis.

3.3.3. Habituation

Several observers noted that habituation of *Pygathrix* species was never achieved (Hoang Minh Duc, 2007; Lippold, 1977; Phaipalath, 2009; Rawson, 2009); some claimed doucs might be impossible to habituate. In some cases, habituation of doucs for study purposes was also not feasible due to the amount of hunting (Coudrat et al., 2012; Phaipalath, 2009). Hunting with guns is not a threat to the doucs of Son Tra, although snare hunting for small animals does occur, and doucs can get trapped in the snares. Gathering detailed information on this species is crucial to inform decision makers better about their needs and the requirements for their survival. Therefore, I decided that the benefit of better understanding the species outweighed the risks of habituation for Son Tra. Despite all predictions, habituation was achieved in this study, although it was a slow process and remained limited. The best habituation was achieved with the primary research group, which ultimately permitted regular observations at close range, accurate home and day range analyses, and recognition of individual doucs. A return trip in 2013 for filming with the British Broadcasting Corporation (BBC), two years after primary research activities ended, confirmed the group was there but was no longer habituated to any degree.

Techniques of habituation followed those outlined by Williamson & Feistner (2003), such as the use of signals (auditory), keeping an observational distance that did not upset the doucs, not pushing the doucs when following them, and waiting at key sites for the doucs rather than searching for them, in addition to avoiding observations from a higher (upslope) position which made them very uncomfortable. Despite the relative success in habituation, the group often (several times a week) did not want to be observed or followed. They also only permitted observations by me and my primary research assistant Mr. Bui Huy Hoang. Any additional observers or other people in their territory were enough to irritate them, and they would remain in hiding, outwaiting the observers.

3.3.4. Observation equipment

All equipment used in this research was purchased from Forestry Suppliers Inc., except where indicated. Observations of doucs were made using the Brunton Echo 50 mm compact spotting scope, 12-36x50. Sampling time was kept using a Nokia cellular phone (Viettel) set to vibrate at 1-min intervals, which was fixed to a clipboard with the behavioral datasheet so that time could be observed constantly and vibration felt easily and heard. As a backup, a field Tech40 Northstar digital watch was worn. No electronic sound signals were used because- based on other wildlife observations I've experienced- even habituated animals can become agitated and alarmed by sudden electronic tones. A Garmin GPSMap 60CSx was used to take UTM locations and permitted most waypoints to be accurate to within a 5 m error. The behavioral datasheet was used for all data records.

3.3.5. Behavioral observations

Animals were classified by sex and age in accordance with data presented in Chapter 2, Tables 2.2 and 2.3. The individual that was in best view was generally selected as the observation subject. Often only one or two individuals were visible at a time due to dense canopy and the dispersion of individuals. Towards the end of research, it was possible to rotate more reliably between group members, a technique noted by Williamson & Feistner (2003). When multiple individuals were encountered, behavioral sampling focused on individuals who were engaged in feeding, as feeding was initially the primary focus of the study. If no animal was engaged in feeding, focus rotated between adult males and females similar to the method outlined in Chapman (1988) and Garber (1988). Behavioral data on subadults, juveniles and infants were only collected when no feeding individual and no adult animal was in sight. Data were gathered on a focal individual for a maximum of 10 min before rotating to a different individual (if one was in sight).

Originally, I planned to use focal animal instantaneous sampling following methods by Altmann (1974) and Campbell et al. (2011), with a 3-min interval. However, during the first six months of data collection, observations were rare with each one lasting no longer than 10 min, and often lasting only a few seconds. I decided to reduce the sampling interval from 3-min to 1-min to increase the amount of data, and because observations in the first six months were so difficult, I was convinced even 1-min intervals would produce only a minimal amount of data. Later on after the primary research group was beginning to be habituated, it presented me with some difficulty in maintaining focal instantaneous sampling at 1-min intervals. Naturally, most samples are not independent, although observations were rotated between individuals every 10 min when possible. Rotation helped to ensure statistical validity of the focal samples, although there is individual and group bias. One-min sampling has been used in other studies (see Chapman & Chapman, 1996; Doran, 1992; Harward, 1977; King et al., 2003; Stone, 2006; Strier, 1997), as has 2-min sampling (see Powzyk & Mowry, 2003). Martin & Bateson (1993) noted that shorter observation intervals allow a more precise representation of activity budgets. King et al. (2003) reported that 1-min intervals allow the recording of more data with no other significant difference compared to 5- or 10-min sampling. Finally, Campbell et al. (2011) noted that the drawbacks to 1-min intervals are that they are both time- and labor- intensive and require a high level of continuous concentration.

As the primary observation group was becoming increasingly habituated, multiple individuals could be seen at the same time, permitting the recording of data on a focal douc with notes to the basic behavioral activities of another nearby douc. Therefore, a reduced form of instantaneous scan sampling was also used to gather additional data specifically on activity budgets when other doucs were visible and near to the focal douc, which enhanced data collection. Focal sampling has been found to be the best method to use with habituated animals (Clutton–Brock, 1977), and this technique, therefore, was maintained throughout the study.

However, the addition of scan sampling allowed me to record activity patterns for multiple individuals without compromising focal behavioral sampling on a focal individual. Also, this did not require a lot of extra time to record. Doran (1992) had illustrated that combining both sampling methods can be beneficial; it allowed me to make the most of the observation possibilities because data were often recorded in short bouts followed by longer periods without visual contact. Furthermore, Hoang Minh Duc (2007) used a similar combination of sampling techniques with black-shanked doucs and, in so doing, gathered exceptional field data.

3.3.6. Behavioral datasheet

Time, weather, GPS location, distance between observer and focal animal and the height of the focal animal in the canopy were recorded on prepared behavioral datasheets. If the focal douc was out of sight, movements and vocalizations were still recorded if they occurred. Unique behaviors or interactions were recorded ad libitum following Campbell et al. (2011). All data were first recorded on field sheets and later transcribed into an Excel spreadsheet. All data used in this study were gathered by me, although I was usually accompanied in the field by field assistants Hoang and Chung from Da Nang University whom I trained in various methods of field observations. I was initially accompanied by two additional students, whom I also trained. Data the students gathered were used for their diploma (BSc) degrees. Given the amount of data recorded and the research foci, not all recorded data were analyzed and presented.

The following data were recorded:

Inactivity:

Many studies do not distinguish between resting and vigilance, although I recorded these behaviors separately. For most analyses, I combined sleeping and resting.

- Sleeping – if the focal douc was observed sleeping between sunset and sunrise.

- Resting – if the focal douc was resting (*i.e.*, sleeping during daytime).
- Vigilance – the focal douc was awake, alert, and scanning the environment but was not involved in any other activity. In most instances the subject watched by the focal douc was also recorded, for example other doucs, the ground, the canopy, or me.

Feeding:

Records include hand placement and food item selection. As noted by Oates (1988b) and Fashing (2001a) feeding involves the selection of leaves or fruits, movements such as bringing the mouth towards a food item or a food item to the mouth, and actively eating (chewing and swallowing).

Hand placements:

- Bringing food item to mouth – which hand or foot held the food item (left, right or both), and if picked, which hand plucked the food item from the twig (left or right) and which hand or foot stabilized the branch.
- Bringing mouth to food item – which hand or foot held the food item steady (left, right or both).

Item of selection:

- Fruits or seeds – it was often not possible to identify if seeds were ingested with mesocarp of fleshy fruits, so these categories were generally not distinguished.
- Flowers – including flower buds.
- Leaves
    - Young leaves – including leaf buds.
    - Mature leaves

  - Unknown leaves – leaves of unknown vegetative phase. This category was often assigned when the canopy obstructed the view.
- Leaf part selected
  - Whole blade – the whole leaf, this may or may not have included the petiole.
  - Blade apices – the upper sections of a leaf blade.
  - Blade bases – the lower sections of a leaf blade, which may or may not have included the petiole.
  - Petioles – stem was selected, and the remaining blade was discarded.
- Other – including only bark and pith.
- Unidentified – if feeding was clearly heard (e.g. biting sounds, food calls) but not observed, or if feeding was observed but the food item selected could not be confirmed because of canopy obstructions or the position of the douc.
- Nursing / breast feeding

Moving:

This category includes foraging movements, social movements, and moving to a resting site and is divided into two subcategories: travel and local movements. Examples of the combination of these subcategories or of their separate analysis (see Garber, 1988) can be found in the literature and appear to be a matter of personal taste. I combined both subcategories in most analyses of this study, so it is comparable with similar studies, but separating the subcategories permits for greater detail. Following Oates (1977), this category does not include any play movements.

- Travel – movements between trees with an apparent destination beyond the immediate 10 m diameter. Feeding and traveling were not mutually exclusive, and often traveling involved feeding as the doucs fed but kept moving to a certain destination. In such cases, the focal subject was only recorded as feeding if the individual was feeding at the moment of instantaneous sampling or as traveling if traveling was observed.

- Local movements – this involved movements often of a meter to 5 m distance, usually occurred within the same tree or to an adjacent tree, and was often combined with feeding or social behaviors. Doucs involved in "local movements" were moving within the general area and not involved in longer distance travel. If it was unclear whether movement was localized or traveling, it was recorded as travel.

Locomotion type:

When a focal douc was moving, the type of locomotion was recorded as long as there was no canopy obstruction.

- Quadrupedal locomotion
- Climbing – this involved vertical climbing and clinging.
- Brachiation
- Jumping – jumps of around 1-5 m but sometimes much more, with a minimal vertical distance (1-3 m). Jumps were generated from the hind-limbs.
- Leap drops – this involved jumps of great vertical distance between starting and landing position often between 5 and 10 m, with a horizontal distance of 5 m at maximum. Doucs "leap dropping" used their arms as a means to position and hold themselves before either letting go and dropping or propelling their body forward, sometimes with considerable force. If it was unclear of the observed locomotion was a jump or leap drop, then it was recorded as a jump.

Social behaviors:

Distance between the focal douc and the next nearest douc was recorded. Various subcategories were distinguished including:

- Grooming – grooming another individual.
- Groomed – groomed by another individual.
- Play – movements clearly performed as a means to have fun or the expression of having fun as described by Oates (1977).
- Copulation – mating or solicitation of mating.
- Vocalization – this involved a number of sub-subcategories comprising the apparent different calls between males and females, and between adults and younger individuals. It also includes several vocalizations of only slight variation that became gradually distinguishable over the duration of research. Often vocalizations involved numerous group members, indicating significance of vocalizations in social interaction.
    - Alarm call and Location call – for both males and females, this is a short loud bark. I suspect there are differences between the alarm and location calls, although I could not discern them. For example, an adult male would sometimes issue what to me seemed to be an alarm call, but the response from the group was to begin traveling rather than hiding, rushing, or otherwise indicating that they are aware or afraid of a threat. At other times, a similar call would be issued in response to a threat, and the group would immediately hide with several individuals joining in the alarm calling.
    - Aggressive calls – this call had an aggressive or territorial meaning. For males this was a long bark, for females a screaming screech or a long bark.

  - Discomfort call – a discomfort call could be submissive or defensive. For males this was a staccato or vibrating grunt, and for females it was a staccato or vibrating whine.
  - Feeding call – for both sexes, this was a low single-toned grunt.
  - Mother call – issued from a mother to her offspring either in response to an infant call or separately, which caused an infant to return to the mother. This call is similar to the adult female discomfort call but is lower in tone and legato.
  - Infant calls – there were a few discernible specific infant / juvenile calls, which are so named because they were only vocalized by young individuals. The easiest to recognize was a discomfort or complaint call; a screeching call that was directed towards the mother often if the infant could not suckle or if the mother was not carrying the infant. The other was a playful screech typically associated with playing between young individuals. These calls were not recorded separately.
  - Other – this included all calls that could not be placed into one of the previous categories.
- Displays and threats – these were distinguished by whom they were directed towards including the sex and age of other douc, if it was a group member, another group, or me. Vocalizations were not recorded here, although certain calls were used during various displays and for threats. Several subcategories of display type were recorded including:
  - Tail display – involved the rapid swinging of the tail left and right.
  - Body / penis display – involved the hanging of the legs below the substrate being sat on and swinging of the tail. For males, this included the display of his testicles

    and erect penis and often involved urination. Females regularly assumed this same posture but were never observed to urinate.
  - Stare display – involved the lowering of the body, extension of the neck forward, flattening of the hair on their forehead and staring at the opposing individual intently.
  - Jumping display – involved rapid quadrupedal movements or jumping within and between trees with relatively forceful use of their limbs, including the shaking of tree branches.
- Other – this involved only auto-grooming behaviors. The body part being groomed was noted and distinction was made between:
  - Grooming or picking of hair.
  - Scratching of skin.

Canopy use:

Most of the forest of Son Tra is disturbed, and the majority of trees are smaller than 20 m in height, although there are patches of good secondary and primary forests with trees reaching 30 m and greater. Canopy use, therefore, was recorded relatively and specifically. This included both the estimation of the height of the douc from the ground in meters and the relative position in the canopy based on the tree they were in and the trees around them. Concerning the relative position, records involved:

- Top / upper canopy – the douc is on the top of the canopy or in the upper portions of the canopy. This was usually more than 20 m above ground.
- Mid-canopy – the douc is in the middle of the canopy. This was usually around 12 to 19 m above ground.

- Lower canopy – the douc is low in the canopy, usually around five to 12 m above ground.
- Ground – the douc is on the ground.

Substrate use:

The type of substrate on which the douc was observed was noted including the diameter and angle for tree branches. Substrates were identified as:

- Branch – stems from the bole or other stems which had additional divisions before leafing.
- Twigs – smaller stems near the end of the canopy of a tree, and which generally lacked divisions before leafing.
- Fork – this is the division of the bole into two or more stems, and the douc would sit at the location of this division.
- Ground – including sitting on a rock or the ground.

3.3.7. Phenology transects

Transects were established to determine resource seasonality, availability, and abundance. Transect establishment and recording followed methods by Ganzhorn (2003) and Vogel & Dominy (2011). Three transects were established: two transects were 300 m long by eight m wide, and one transect was 500 m long by eight m wide. Similar transects were used in studies such as Chapman & Chapman (1996), Fimbel et al. (2001) and Rode et al. (2003) who all used transects measuring 200 x 10 m, and Rawson (2009) who established 500 x 10 m and 300 x 10 m transects.

Line transects were used rather than plots because of the mixed character of forests on Son Tra. According to Ganzhorn (2003), line transects are more appropriate in forests with patchy distributions of trees. White & Edwards (2000) suggested that using line transects results in cataloging edge effects more so than using plots. However, edge effects were not observed in this study despite using line transects.

Location of transects was determined using a random number generator in Microsoft Excel for UTM coordinates in tandem with a number generated for direction of the transect from the starting point (from 0.1 to 360 degrees with 360 degrees representing the cardinal direction of due north). If both the randomly generated UTM coordinate and the direction allowed the transect to be included entirely within Son Tra Peninsula and did not extend into the coastal area, military areas, business areas, or eucalyptus plantation forests then it was used. Van Peenen et al. (1971) noted that doucs were observed in most forests on Son Tra, so there were no additional habitat limitations placed on where or in which directions transects would occur. Whether or not a transect would approach or cross a road was not a determining factor in transect locations. However, no transect crossed a road, although two approached a road.

Transect starting positions were located in the forest with the GPS, and the direction was maintained using a Kasper & Richter Meridian Pro Sighting Compass. Measuring transect length and width was done with a Keson Ultra-glass Open Reel Fiberglass 30-m tape measure and a Stanley PowerLock 10-m tape measure. Straight lines were established using the 30-m tape measure stretched out along the directional line. This usually occurred for about 10 m before a tree, boulder, crevasses, or steep incline or decline required us to stop, move forward, reestablish the line and continue behind the obstacle. On each side of the transect mid-line, 4 m were measured. All trees with a DBH of 10 cm or more were tagged and included in the analyses. If a tree’s trunk was 50% or more within the transect width, it was included in the transect analysis following recommendations from White & Edwards (2000) who argued this reduces edge effects in transects.

During transect establishment, there was little to no cutting because I did not want to create an accessible trail for people entering Son Tra illegally. Vegetation was left untouched except for some very dense areas where cutting was kept to a minimum.

During transect establishment, I recorded elevation every 5 m using the Garmin GPSmap CSx. Every 5 m, I also recorded the percentage (0-100%) of light on the transect mid-line using a densitometer, with 0% corresponding to no light and therefore dense tree canopy and with 100% corresponding to full light and completely open sky. This allows for a basic analysis of the general openness of the canopy and the amount of light reaching the understory. Elevation and light data were taken starting at the 0 m mark and ending at the end of the transect (300 or 500 m mark).

Each tree was recorded for its distance from the starting point of the transect and its distance to the left or right of the transect mid-line. Each tree was measured initially for DBH, height, and crown width. The height of trees was estimated using the 10-m tape measure. If a tree was taller than 10 m, the tape measure was extended as far as possible and the remaining height estimated. This technique worked well as most trees were small. A range finder would have been more accurate; however, for tall trees a range finder still requires one to stand directly under the tree and point the laser at the highest point on the tree. Rawson (2009) noted that the range finder often required additional estimates and could not be used with Pythagoras' Theorem because measuring accuracy decreased with the height of the tree.

Crown width of trees was measured by locating the widest distance between twigs visually on the same horizontal plane, standing directly under these twigs and measuring to the tree trunk using the tape measures. Diameter of the trunk was then added to the measurement.

All trees with a DBH of ≥ 10 cm were included in accordance with Ganzhorn (2003). Lianas were not included in this analysis, although a few had large diameters. Future studies on Son Tra would benefit from including these into analyses, perhaps even decreasing the DBH for lianas similar to Matsuda (2008). Breast height in this study was 1.3 m (my chest height), which is also most widely used in primate studies and in the field of forestry (Hédl et al., 2009; Reid & Stephen, 2001). All measures of DBH were taken with the Spencer Chrome-clad Logger's Tree Diameter tape measure. If a tree trunk began to fork before breast height, then DBH was taken on the larger of the two branches but only if DBH of the larger branch was ≥ 10 cm. Much of the terrain on Son Tra is sloped, so breast height was always measured from downslope.

I recorded the phenophases of each tree (van Schaik et al. 1993) including young leaves, mature leaves, dead or dying leaves, fruits, and flowers. Phenophases were recorded as percentage of young leaves to mature leaves (out of 100% total leaves), percentage of dead or dying leaves to living leaves (out of 100% total leaves), and the approximate amount of the leaf canopy bearing fruit (out of 100%) and flowers (out of 100%). These values were estimated after a tree was surveyed from each side. Milton (1984b) and Fashing (2001a) used similar percentages in their studies. Ganzhorn (2003) and Chin Sun et al. (1996) suggested recording transect data along a point scale, which relates to percentages. The way I gathered transect data permits comparison with point scale data but allows for more detailed and refined analyses. Each tree was recorded on the GPS and tagged with a small, inconspicuous aluminum tag (1.25 in. diameter). I aimed to keep transects undetectable. Aluminum tags are commonly used in long-term studies to reduce damage to trees caused by rust (Ganzhorn, 2003; Chin Sun et al., 1996). After the identification of all trees and the completion of the monitoring period, all tags and nails were removed.

Transect tree identification was done by Nguyen Thi Dao, a botanist working at Da Nang University, and Tran Ngoc Toan, a botanist working in Kon Ka Kinh National Park. Nguyen Thi Dao worked as a botanist for a comprehensive biodiversity assessment of flora on Son Tra (Dinh Thi Phuong Anh, 1997), and she recommended Tran Ngoc Toan for this study as one of her former students. Tree identification was done primarily in the forest, but catalogues, photographs, and plant samples were consulted when necessary. Transect trees were only identified to family level due to the cost of tree identifications, whereas feeding trees were identified to species level. All trees were identified by Ms. Dao and Mr. Toan. If they did not feel confident with a particular identification, they provided an estimate with the nomenclature *cf* to indicate uncertainty.

Transects were monitored for 13 months, from May 2010 through May 2011. Each transect was recorded twice a month at 2-week intervals as recommended by Ganzhorn (2003) and Sayers & Norconk (2008). Monitoring twice per month allows for a more detailed analysis of seasonality and food availability (Stevenson et al., 1998) compared to monitoring once a month, although most studies only analyze transects once per month. There were a few exceptions to monitoring transects twice per month: in May 2010 transects were recorded once due to transect establishment, in June 2010 Transect 3 was analyzed once to avoid scheduling conflicts, and in July 2010 Transect 1 and 3 were only recorded once. As all transects were analyzed once in May 2010 and twice in May 2011, May represents the month with the most robust transect record.

3.3.8. Food trees

During feeding observations, the selected food item was recorded if this was clearly observed (*i.e.*, not obstructed by the canopy or the position of the douc). In some cases, it was clear that feeding was occurring despite a lack of visual contact (*i.e.*, biting of a hard fruit, seed, or bark could be heard, and food calls could be heard at close distance). In these cases, I searched for secondary evidence of feeding similar to McGrew et al. (1988), namely partially-eaten material on the ground below the spot where the douc was seen or heard. However, if the doucs were traveling with macaques or if the macaques were heard or seen within 100 m, then all secondary evidence was rejected. Only freshly bitten secondary evidence was used. All secondary evidence accounted for 5% of food species records and contributed no new food species. When secondary evidence was found and used, the nearest tree which produced the resource was located and given a GPS waypoint.

For each feeding observation, the location of the feeding tree was given a GPS waypoint. For the primary research group, feeding occurred in many of the same trees throughout the research, and waypoints were not necessary to record each time. Trees were not marked with tags or paint because I did not want to draw attention of plant collectors to these trees, I was not sure how the doucs would react to feeding trees being marked, and I sought to reduce interruption to the natural environment.

Data collected on feeding trees included:

- GPS location – each tree was given a unique name based on the date and sequential numbering system.
- Height – measured in the same way as with transect trees.
- Crown width - measured in the same way as with transect trees.
- DBH – measured in the same way as with transect trees.
- Proportions of young leaves, mature leaves, fruits, and flowers (measured in the same way as with transect trees).

- Plant sample collection for identification – leaves, fruit and flowers were collected, photographed and pressed using the Forestry Suppliers Standard Plant Press kit with Standard Drying Cards for absorbing moisture. All samples were labeled. Sample drying occurred inside and was assisted with silica gel in an air-conditioned room, both of which reduced moisture content. Samples were often collected by climbing into the tree, but this occurred at a later date and not immediately following an observed feeding bout when the doucs were in the vicinity. Fruits and flowers were frequently collected from the ground after they were dropped by the doucs.
    - Plant samples were also collected for nutritional analysis (see section 3.3.9)
- Tree species identification – conducted in the same manner as transect trees, although these trees were always identified to species level.

3.3.9. Chemical and nutritional samples and testing

Samples were tested for chemical and nutritional quality. As noted by Chapman et al. (2003), only the plant part which was observed to have been consumed was collected. Samples were collected from the trees on which the feeding observations were made as suggested by Ortmann et al. (2006) and Rothman et al. (2012). Chapman et al. (2003) and Houle et al. (2007) noted that chemical and nutritional quality of food items can differ between individual trees of one species and within a tree at different times of day. Ortmann et al. (2006) recommended collecton of samples immediately following an observed feeding bout due to changes in chemistry throughout a day. I followed these methods as far as possible, although it was not usually possible to collect leaf samples from the exact part of the tree the doucs had been feeding because the doucs mostly fed in the upper canopy, which I could not access. Sometimes food items (fruit, flowers, stems) were not abundant within a tree, and collection of enough material for analysis would have caused serious damage to the tree. This is not acceptable for the tree or the doucs, and in these cases, samples had to be collected from two or more trees. Finally, it was not possible to collect samples directly following a feeding observation because preference was given to following the doucs, although samples were collected at the same time of day of the feeding observation within two weeks.

Samples were weighed on site immediately after collection for an accurate measure of water content. They were brought home and spread out in an air-conditioned room to dry. They were kept out of the sunlight following suggestions by Lucas et al. (2003), Rode et al. (2003), Rothman et al. (2012) and Wasserman & Chapman (2003). Drying samples at low temperatures or with the aid of silica gel has been recommended by Lucas et al. (2003) who illustrated that drying plant samples in sunlight or high temperature results in significant changes to plant chemistry. Samples were dried for at least two weeks, then weighed again, then left for another week and weighed a third time. If the second and third weights were identical, then the sample was considered dry and was stored in a plastic container with silica gel. If the sample was still decreasing in weight, it was considered to retain water and was left for an additional week and then weighed again. All samples were weighed a final time before being transported to the laboratory for analysis to ensure that dry weight was still the same.

It was initially estimated that an amount of 100 grams of fresh matter was sufficient for chemical testing, based on previous studies. However, the laboratory I used required over twice this amount and in dry matter. Luckily, 22 of my samples met this criterion, but 23 samples had to be discarded. This does not represent the full range of food species observed to be eaten (N=62). Analysis was conducted at the laboratory of the Research Institute for Biotechnology and Environment at Nong Lam University in Ho Chi Minh City. Five values were tested for, including crude protein, ash, condensed tannins, NDF and ADF.

Water content was measured as noted above. Mass of 1 ml of water is 1 gr., therefore water content is reported as ml of water per gr. of dry weight. All other tests were conducted by the Research Institute for Biotechnology and Environment. Samples were ground by a Wiley mill and passed through a 1 mm wire screen, similar to the technique of Hoang Minh Duc (2007) and Workman (2010). For quality control, each test was conducted twice, and results reported represent the average of the two tests.

Testing for ash (dry matter) followed the AOAC 935.12-2000 methodology. Testing for condensed tannins followed the AOAC & TC 2000 methodology. Testing for crude protein followed the Kjeldahl (AOAC 984.13) methodology (see Horowitz, 1970). This included the nitrogen x 6.25 conversion factor noted by Maynard and Loosli (1969). There are currently no AOAC methods for testing NDF content; therefore testing for NDF followed the methodology used by the U.S. Department of Agriculture, as outlined by Goering & van Soest (1970) and van Soest et al. (1991). NDF provides a measure of lignin, hemicellulose and cellulose in the sample. Testing for ADF followed the AOAC 973.18 methodology, and this provides a measure of indigestible fibers (lignin and lignin coated cellulose).

3.3.10. Research schedule and data

Research was scheduled for 20 days each month from February 2010 through May 2011. Following this, activities centered on conservation, conservation education, and student field training. Field data were also collected from June 2011 through March 2012, although I infrequently accessed the forest during this time, and when I did, I only collected data on feeding. These data only contribute four feeding species that were not observed in the previous years and are otherwise not analyzed. Concerning the primary field research period (February 2010 through May 2011), I spent a total 1619 hours in the field, 259 hours of which were in contact with the doucs. This yielded 15,528 min of analyzable data. This robust sample is due to the success in habituation and the 1-min sample intervals used. This study had 218 separate encounters with douc groups. This is a smaller amount than some *Pygathrix* studies because I recorded multiple encounters on the same day with the same group or unit as a single encounter, and because as the primary research group became a focus, my encounters with other groups were reduced.

Chapter 4. Transects: forest characteristics and phenology

4.1. Introduction

4.1.1. Study and chapter preview

Establishing phenology transects and monitoring plant phenology helps to better understand primate and plant relationships. Phenology transects record the seasonal fluctuations in plant fruiting and leafing cycles and the relative availability of food items for consumers (Ganzhorn, 2003; van Schaik et al., 1993).

This chapter describes the phenology of three transects used during research activities, relates the phenology data to weather patterns, and later relates these to ranging and social behavior (Chapter 5), activity patterns (Chapter 6), and feeding behavior (Chapter 7). Following a review of forest characteristics and methods, results are reported for transect tree family diversity, height, DBH, crown width, canopy density, stand basal area and tree density, tree mortality, phenophase patterns (leaf flush, leaf fall, flowering and fruiting), masting and *Parashorea stellata* phenology.

4.1.2. Forest characteristics

Son Tra can be characterized as a semi-evergreen seasonal forest which Wright (1996) noted as a forest type with eight to 10 months of rainfall exceeding evapotransporation (60 mm). As noted in Chapter 3, monthly precipitation on Son Tra fluctuated from 0 to 825 mm although areas on Son Tra above 300 m experience a greater amount of rain. Therefore, Son Tra might be compared to both dry and wet tropical forests. However, given that the average annual precipitation recorded at the base of Son Tra is less than 2500 mm, which Murphy & Lugo (1986) noted is necessary for categorization as wet tropical forest, Son Tra as per classification is considered a dry tropical semi-evergreen forest.

Numerous studies have reported on the phenology patterns among seasonally dry and wet forests, relating them to irradiance, water stress, seedling mortality, and herbivory (see Aide, 1988; Borchert, 1983; Corlett & La Frankie, 1998; Daubenmire, 1972; Frankie et al., 1974; Lieberman, 1982; Murphy & Lugo, 1986; Reich & Borchert, 1984; Tissue & Wright, 1995; van Schaik, 1986; van Schaik et al., 1993; Wright, 1991; Wright, 1996; Wright & van Schaik, 1994) . Naturally, phenology cycles are in a constant flux (Newstrom et al., 1994; van Schaik et al., 1993; Wright, 1996), and patterns can differ significantly even within a forest (Sakai, 2001).

Availability and seasonality of resources greatly influences primate ecology, and van Schaik et al. (1993) noted that primates respond to resource availability with dietary changes, changes in ranging, activity, migrations, or seasonal birthing. Keystone resources are critical in times of food scarcity. However, correlations between phenology and primate behavior differ remarkably between species. For example, ranging behavior among *C. satanas* (Oates, 1994), *S. dussumieri (entellus)* (Sayers & Norconk, 2008), *T. pileatus* (Oates, 1994), *R. bieti* (Qikun Zhao, 1988), and *P. nigripes* (Hoang Minh Duc, 2007) increases during fruiting peaks and it has been suggested this is to exploit more widely dispersed high quality foods. In contrast, ranging decreased during fruiting peaks for *N. larvatus* (Matsuda, 2009b) and *P. nemaeus* (Phiapalath, 2009), possibly because high quality foods would permit daily energy requirements to be met more quickly. Activity patterns in *C. polykomos* (Dasilva, 1989), *T. francoisi* (Qihai Zhou et al., 2007), *R. bieti* (Wei Ding & Qi-Kun Zhao, 2004) and *R. roxellana* (Songtao Guo et al., 2007) showed less resting and more traveling during times of preferred food abundance to exploit dispersed resources. During times of high quality food availability, traveling and resting increase for *P. nigripes* (Hoang Minh Duc, 2007), and travel decreases and resting increases in *P. cinerea* (Ha Thang Long, 2009) and *P. nemaeus* (Phiapalath & Suwanwaree, 2010).

Seasonal breeding in mammals has been shown to be correlated with phenological cycles (Snow, 1965), including among a variety of colobine primates (Baoguo Li & Dapeng Zhao, 2007; Dasilva, 1992; Koenig et al., 1997; Liang-Wei Cui et al., 2006; Newton, 1988; Shuyi Zhang et al., 2000; Tong Jin et al., 2009) and has been suggested for the red-shanked douc (Lippold, 1977; Phiapalath et al., 2011). Knowledge of a primate species' key food resources, their availability and phenological cycles is important in conservation because of the co-dependency of primates and plants (Chapman & Onderdonk, 1998). As noted in van Schaik et al. (1993), only a few exploited plants produce edible resources all year and distinguishing these keystone resources requires long-term studies and thorough knowledge of local flora and phenological patterns.

4.2. Methods

Methods of transect establishment were described in Chapter 3. The list of species is presented in Table 4.1. Table 4.2 lists the number of trees in each transect and the elevation at the start and end point of each transect. Figure 4.1 shows the transect locations.

Transect trees are compared for values (height, crown width, DBH, canopy density) both descriptively and quantitatively. This allows a general exploration of habitat types and habitat use by the doucs in later chapters. Data for tree height, crown width and DBH are nominal, and means are therefore compared using a one-way Analysis of Variance (ANOVA) with p=0.05. Because variances of these variables are not equal between transects, values are log transformed using the natural log. This is acceptable when variances are dissimilar, allowing for a more robust statistical comparison and permitting assumptions of normalcy associated with parametric analyses to be met. For crown width and DBH, Scheffé Least Significant Difference post- hoc test was used. This was used instead of Tukey's post- hoc test because sample size differed between transects. Scheffé post- hoc test also requires a larger least significant difference and is therefore considered more robust than Tukey's test. Stand Basal Area (SBA) is compared, which is the amount of the transect area covered by measured trees. SBA for trees is calculated using the formula SBA in $m^2 = (DBH/200)^2 \times 3.14159$. Total SBA of all trees in each transect is calculated using the sum of the SBA in m^2 per transect plot area in ha (m^2/ha). Transect 1 covers 4000 m^2 or 0.4 ha, and Transects 2 and 3 each cover 2400 m^2 or 0.24 ha. Density is calculated as the number of transect trees divided by the area (trees/ha).

Comparisons between transects for fruiting, flowering, leaf flush and leaf fall allow for comparisons of overall phenological patterns on Son Tra and for assessment of the variation between transects. They also allow for comparison with behavior in later chapters. These comparisons generally involve combining all transect data, and testing for significant differences between seasons using the two proportion z-test with 95% confidence because phenophase data were gathered as percentage or ratio and not ranks. Non-parametric analyses can be conducted by transforming percentage data to rank data; however parametric analyses are preferential because they allow for more strict statistical comparisons. Comparisons between transects involved the three independent-group proportion z-test with significance placed at 95% confidence. Due to the degree of data, non-significant values are not usually reported. Finally, comparisons of phenophase patterns to weather patterns involved Pearson's Correlation Coefficient. This was chosen because data were ratio based, the analysis is parametric based and this correlation analyzes linear relations (*i.e.*, an increase or decrease in temperature or precipitation causes either an increase or decrease in forest productivity). All correlations are two-sided with a significance set at $p=0.05$.

Transect trees were not identified to species, and this precluded analyses of species richness, species diversity and species evenness between transects. However, family-level diversity is compared.

Table 4.1. Identifications of transect trees.
Identifications to family level with genera and / or species identification provided in parentheses if available. An identification preceded by *cf.* indicates uncertainty of identification, and indet. indicates an unidentified family.

	Transect 1	Transect 2	Transect 3
Number	Family (genus or species)	Family (genus or species)	Family (genus or species)
1	Sapindaceae	Sapotaceae	Fagaceae (*Lithocarpus*)
2	Dipterocarpaceae (*Parashorea stellata* Kurz.)	Anacardiaceae	Ebenaceae
3	Fagaceae	Anacardiaceae (*G. wrayi* King)	Lauraceae (*Cinnamomum)*
4	Bombacaceae	Araliaceae (*Scheflera bodoni*)	Fagaceae (*Lithocarpus*)
5	Myrtaceae	*cf.* Sapindaceae	Verbenaceae
6	Fabaceae	Sapotaceae	Sterculiaceae
7	Dipterocarpaceae (*P. stellata* Kurz.)	Anacardiaceae	Sapindaceae
8	Dipterocarpaceae (*P. stellata* Kurz.)	Ebenaceae	Rutaceae
9	Euphorbiaceae	Myrtaceae	Rutaceae
10	Euphorbiaceae (*Baccaurea ramiflora* Lour.)	Sapotaceae	Myrtaceae
11	Guttiferae	Anacardiaceae (*G. wrayi* King)	Sterculiaceae
12	Moraceae	Anacardiaceae (*G. wrayi* King)	Anacardiaceae (*G. wrayi* King)
13	Guttiferae	Anacardiaceae (*G. wrayi* King)	Sapindaceae
14	Flacourtiaceae	Anacardiaceae (*G. wrayi* King)	Sterculiaceae
15	Meliaceae	Euphorbiaceae (*Baccaurea ramiflora* Lour.)	Sapindaceae
16	Myrtaceae	Anacardiaceae (*G. wrayi* King)	*cf.* Lauraceae
17	Euphorbiaceae	Myrtaceae (*Syzygium*)	Myrtaceae
18	Ebenaceae	Euphorbiaceae	Ebenaceae
19	Rubiaceae	Euphorbiaceae	*cf.* Lauraceae
20	Ulmaceae	Euphorbiaceae	Myrtaceae (*Syzygium*)
21	Euphorbiaceae	Euphorbiaceae	Myrtaceae
22	Euphorbiaceae	Sterculiaceae	Sterculiaceae
23	Euphorbiaceae	Euphorbiaceae	Euphorbiaceae (*Mallotus floribundus* Blume. Muell.Arg.)
24	Euphorbiaceae	Euphorbiaceae	Burseraceae
25	Olacaceae	Ebenaceae	Ebenaceae
26	Lauraceae	Guttiferae (*Garcinia oblongifolia* Champ. ex Benth)	Ebenaceae
27	Dipterocarpaceae (*P. stellata* Kurz.)	Flacourtiaceae	Euphorbiaceae
28	Myrtaceae	Tiliaceae	Sterculiaceae
29	Euphorbiaceae	Flacourtiaceae	Sapindaceae
30	Euphorbiaceae	Annonaceae	Cycadaceae (*Cycas inermis* Lour.)
31	Myrtaceae	Lauraceae	Ebenaceae
32	Myrtaceae	Anacardiaceae	Olacaceae

33	Dipterocarpaceae (*P. stellata* Kurz.)	Lauraceae	Cycadaceae (*Cycas inermis* Lour.)
34	Burseraceae	Ebenaceae	Sapindaceae
35	Lauraceae	Euphorbiaceae (*B. ramiflora* Lour.)	Olacaceae
36	Euphorbiaceae	Tiliaceae	Euphorbiaceae
37	Annonaceae	Fabaceae (*Sindora tonkinensis* A. Chev. Ex K. Lars, S. Lars.)	Sapindaceae
38	Lauraceae	Fabaceae (*Dalbergia bariensis* Pierre.)	Olacaceae
39	*cf.* Lauraceae	Ebenaceae	Sapindaceae
40	Anacardiaceae	Euphorbiaceae (*B. ramiflora* Lour.)	Sapindaceae
41	Dipterocarpaceae (*P. stellata* Kurz.)	Myrtaceae	Lauraceae
42	Dipterocarpaceae (*P. stellata* Kurz.)	Euphorbiaceae	Ebenaceae
43	Dipterocarpaceae (*P. stellata* Kurz.)	Euphorbiaceae	Rutaceae
44	Myrtaceae	Anacardiaceae	Ebenaceae
45	Tiliaceae	Symplocaceae	*cf.* Flacourtiaceae
46	Annonaceae	Euphorbiaceae (*B. ramiflora* Lour.)	Fagaceae
47	Lauraceae	Anacardiaceae	Olacaceae
48	Myrtaceae	Fabaceae (*D. bariensis* Pierre.)	Myrtaceae
49	Euphorbiaceae	Euphorbiaceae	Sapindaceae
50	Dipterocarpaceae (*P. stellata* Kurz.)	Euphorbiaceae (*B. ramiflora* Lour.)	Myrtaceae
51	Dipterocarpaceae (*P. stellata* Kurz.)	Anacardiaceae (*G. wrayi* King)	Sapindaceae
52	Lauraceae	Euphorbiaceae	Sapindaceae
53	Flacourtiaceae	Anacardiaceae	Sapindaceae
54	Dipterocarpaceae	Araliaceae	Ebenaceae
55	Myrtaceae	Anacardiaceae	Myrtaceae
56	Myrtaceae	Burseraceae	Myrtaceae
57	Rubiaceae	Euphorbiaceae	Sterculiaceae
58	Dipterocarpaceae (*P. stellata* Kurz.)	Anacardiaceae (*Semecarpus reticulata* Lec.)	Sapindaceae
59	Euphorbiaceae	Euphorbiaceae (*B. ramiflora* Lour.)	Myrtaceae
60	Myrtaceae	Myrtaceae	Guttiferae
61	Tiliaceae	Anacardiaceae	Euphorbiaceae
62	Euphorbiaceae	Euphorbiaceae	Ebenaceae
63	Dipterocarpaceae (*P. stellata* Kurz.)	Euphorbiaceae (*B. ramiflora* Lour.)	Theaceae
64	Elaeocarpaceae	*cf.* Styracaceae	Myrtaceae
65	Myrtaceae	Myrtaceae	Lauraceae
66	Tiliaceae	Euphorbiaceae (*B. ramiflora* Lour.)	Ebenaceae
67	Dipterocarpaceae (*P. stellata* Kurz.)	Ebenaceae	Myrtaceae
68	Dipterocarpaceae (*P. stellata* Kurz.)	Anacardiaceae	Sapindaceae

69	Dipterocarpaceae (*P. stellata* Kurz.)	Myrtaceae	Guttiferae
70	Elaeocarpaceae	Annonaceae	Sterculiaceae
71	Anacardiaceae	Sapindaceae	Sterculiaceae
72	Annonaceae	Guttiferae (*G. oblongifolia* Champ. ex Benth)	Sterculiaceae
73	Sapindaceae	Myrtaceae	Sapindaceae
74	Guttiferae (*Garcinia oblongifolia* Champ. ex Benth)	Euphorbiaceae (*B. ramiflora* Lour.)	indet.
75	Myrtaceae	Melastomaceae	Guttiferae
76	Anacardiaceae (*Semeocarpus*)	Tiliaceae	Myrtaceae
77	Anacardiaceae (*Semeocarpus*)	Myrtaceae	Sapindaceae
78	Fagaceae	Euphorbiaceae (*B. ramiflora* Lour.)	Euphorbiaceae
79	Euphorbiaceae	Araliaceae	Rutaceae
80	Moraceae	Anacardiaceae	*cf.* Fabaceae
81	Dipterocarpaceae (*P. stellata* Kurz.)	Euphorbiaceae	Euphorbiaceae (*B. ramiflora* Lour.)
82	Euphorbiaceae	Euphorbiaceae	Sapindaceae
83	Myrtaceae	Euphorbiaceae (*B. ramiflora* Lour.)	Sapindaceae
84	Sapindaceae	Guttiferae	Ebenaceae
85	Dipterocarpaceae (*P. stellata* Kurz.)	Melastomaceae	Lauraceae
86	Dipterocarpaceae (*P. stellata* Kurz.)	Fabaceae	Lauraceae
87	Myrtaceae	Euphorbiaceae	Sapindaceae
88	Guttiferae	Moraceae	Tiliaceae
89	Dipterocarpaceae (*P. stellata* Kurz.)	Melastomaceae	Tiliaceae
90	Euphorbiaceae	Euphorbiaceae	Sterculiaceae
91	Dipterocarpaceae (*P. stellata* Kurz.)	Euphorbiaceae (*B. ramiflora* Lour.)	Sterculiaceae
92	Rubiaceae	Myrtaceae	Sterculiaceae
93	Anacardiaceae (*Semeocarpus*)	Euphorbiaceae (*B. ramiflora* Lour.)	Myrtaceae
94	Tiliaceae	Euphorbiaceae (*B. ramiflora* Lour.)	Moraceae
95	Dipterocarpaceae (*P. stellata* Kurz.)	Ebenaceae	Sapindaceae
96	Guttiferae	Anacardiaceae	Sapindaceae
97	Melastomaceae	Euphorbiaceae	Euphorbiaceae
98	Dipterocarpaceae (*P. stellata* Kurz.)	Euphorbiaceae	Sapindaceae
99	Dipterocarpaceae	Moraceae (*Ficus depressa Blume)*	Sterculiaceae
100	indet.	Euphorbiaceae	Lauraceae
101	Olacaceae	Euphorbiaceae (*B. ramiflora* Lour.)	Euphorbiaceae (*B. ramiflora* Lour.)
102	Tiliaceae	Ebenaceae	Melastomaceae
103	Sapindaceae	Myrtaceae	*cf.* Lauraceae
104	Olacaceae	Anacardiaceae	Sapindaceae
105	Dipterocarpaceae (*P. stellata* Kurz.)	Myrtaceae	Ebenaceae

106	Anacardiaceae (*Semeocarpus*)	Flacourtiaceae	Sapindaceae
107	Fagaceae		Ebenaceae
108	Olacaceae		Lauraceae
109	Sapindaceae		Rutaceae
110	Olacaceae		Sapindaceae
111	Cycadaceae (*Cycas inermis* Lour.)		Ebenaceae
112	Olacaceae		Euphorbiaceae
113	Dipterocarpaceae (*P. stellata* Kurz.)		Sapindaceae
114	Moraceae (*Ficus*)		Ebenaceae
115	Lauraceae		Myrtaceae
116	Euphorbiaceae		Annonaceae
117	Cycadaceae (*Cycas inermis* Lour.)		Lauraceae
118	Olacaceae		Sterculiaceae
119	Olacaceae		Tiliaceae
120	Olacaceae		Moraceae
121	Anacardiaceae		Ebenaceae
122	Rubiaceae		Fagaceae
123	Euphorbiaceae		Euphorbiaceae
124	Euphorbiaceae		Fagaceae
125	Dipterocarpaceae (*P. stellata* Kurz.)		Sterculiaceae
126	Myrtaceae		Burseraceae
127	Euphorbiaceae (*Mallotus floribundus* Blume. Muell.Arg.)		Burseraceae
128	Rubiaceae		Sapindaceae
129	Myrtaceae		Burseraceae
130	Myrtaceae		Fagaceae
131	Rubiaceae		Myrtaceae
132	Myrtaceae		Myrtaceae
133	Myrtaceae		Lauraceae (*Cinnamomum*)
134	Dipterocarpaceae (*P. stellata* Kurz.)		Euphorbiaceae
135	Sapindaceae		Anacardiaceae
136	Cycadaceae (*Cycas inermis* Lour.)		Lauraceae
137	Fabaceae		Myrtaceae
138	Dipterocarpaceae		Euphorbiaceae
139	Fagaceae		Lauraceae
140	Lauraceae		Lauraceae
141	Myrtaceae		indet.
142	Cycadaceae (*Cycas inermis* Lour.)		Myrtaceae
143	Sapindaceae		Euphorbiaceae
144	Sapindaceae		Myrtaceae
145	Dipterocarpaceae (*P. stellata* Kurz.)		Euphorbiaceae
146	Anacardiaceae (*Semeocarpus*)		Dipterocarpaceae
147	Dipterocarpaceae (*P. stellata* Kurz.)		Euphorbiaceae (*Mallotus floribundus* Blume. Muell.Arg.)
148	Myrtaceae		Euphorbiaceae
149	Myrtaceae		Tiliaceae

150	Flacourtiaceae		Lauraceae
151	Dipterocarpaceae (*P. stellata* Kurz.)		Myrtaceae
152	Dipterocarpaceae (*P. stellata* Kurz.)		Sapindaceae
153	Rubiaceae		Sapindaceae
154	Euphorbiaceae		Euphorbiaceae
155	Dipterocarpaceae (*P. stellata* Kurz.)		Sapindaceae
156	Flacourtiaceae		Euphorbiaceae
157	Loganiaceae		Euphorbiaceae
158	Lauraceae		Myrtaceae
159	Lauraceae (*Cinnamomum*)		Myrtaceae
160	Euphorbiaceae (*M. floribundus* Blume. Muell.Arg.)		Verbenaceae
161	Guttiferae		Ebenaceae
162	Tiliaceae		*cf.* Euphorbiaceae
163	Dipterocarpaceae (*P. stellata* Kurz.)		Euphorbiaceae
164	Tiliaceae		Euphorbiaceae
165	Sterculiaceae		indet.
166	Rubiaceae		Euphorbiaceae
167	Dipterocarpaceae (*P. stellata* Kurz.)		Euphorbiaceae
168	Myrtaceae		Moraceae (*Ficus*)
169	Fagaceae		Euphorbiaceae
170	Fagaceae		Sapindaceae
171	Dipterocarpaceae		
172	Lauraceae (*Cinnamomum*)		
173	Dipterocarpaceae (*P. stellata* Kurz.)		
174	Rubiaceae		
175	Rubiaceae		
176	Flacourtiaceae		
177	Styracaceae		
178	Anacardiaceae		
179	Myrtaceae		
180	Euphorbiaceae (*B. ramiflora* Lour.)		
181	Euphorbiaceae (*M. floribundus* Blume. Muell.Arg.)		
182	Guttiferae		
183	Lauraceae		
184	Tiliaceae		
185	Ebenaceae		
186	Dipterocarpaceae (*P. stellata* Kurz.)		
187	Anacardiaceae (*Semeocarpus*)		
188	Verbenaceae		
189	Dipterocarpaceae		
190	Sterculiaceae		
191	Euphorbiaceae		
192	Sterculiaceae		
193	Dipterocarpaceae		

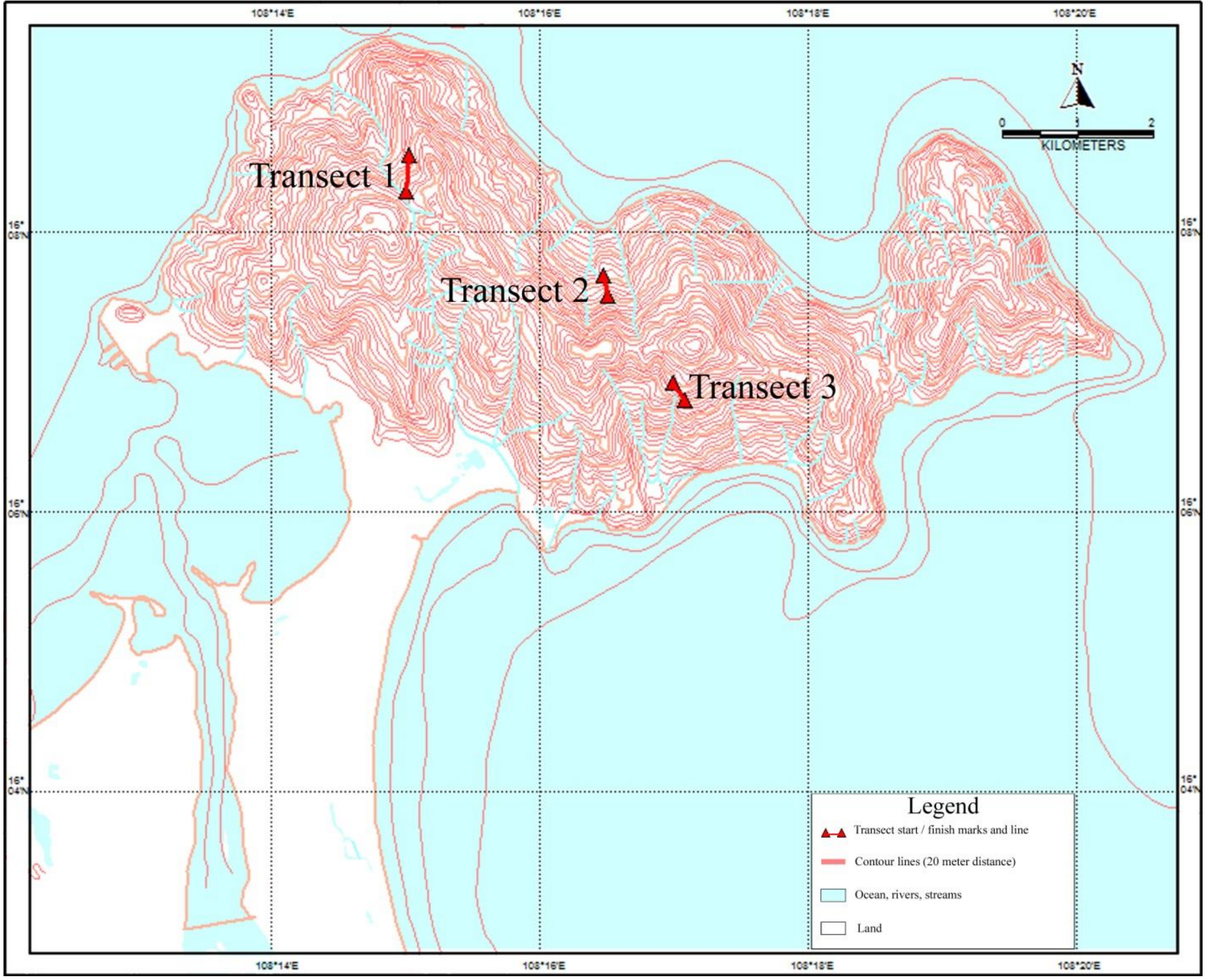
194	Flacourtiaceae		
195	Euphorbiaceae (*B. ramiflora* Lour.)		
196	Cycadaceae (*Cycas inermis* Lour.)		
197	Guttiferae (*G. oblongifolia* Champ. ex Benth)		
198	Dipterocarpaceae (*P. stellata* Kurz.)		
199	Euphorbiaceae (*B. ramiflora* Lour.)		
200	Euphorbiaceae (*B. ramiflora* Lour.)		
201	Dipterocarpaceae (*P. stellata* Kurz.)		
202	Lauraceae		
203	Melastomaceae		
204	Verbenaceae		
205	Anacardiaceae (*Semeocarpus*)		
206	Sterculiaceae		
207	Anacardiaceae (*Semeocarpus*)		
208	Cycadaceae (*Cycas inermis* Lour.)		
209	Anacardiaceae (*Semeocarpus*)		
210	Dipterocarpaceae (*P. stellata* Kurz.)		
211	Dipterocarpaceae (*P. stellata* Kurz.)		
212	Meliaceae		
213	Meliaceae		
214	indet.		
215	Dipterocarpaceae (*P. stellata* Kurz.)		
216	Flacourtiaceae		
217	Cycadaceae (*Cycas inermis* Lour.)		
218	Lauraceae		
219	Lauraceae		
220	Cycadaceae (*Cycas inermis* Lour.)		
221	Verbenaceae		
222	Verbenaceae		
223	Fagaceae		
224	Burseraceae		
225	Fagaceae		
226	Dipterocarpaceae (*P. stellata* Kurz.)		
227	*cf.* Styracaceae		
228	Sapindaceae		
229	Euphorbiaceae (*B. ramiflora* Lour.)		
230	Flacourtiaceae		
231	Euphorbiaceae (*B. ramiflora* Lour.)		

232	Flacourtiaceae		
233	Dipterocarpaceae (*P. stellata* Kurz.)		
234	Myrtaceae		
235	Sapindaceae		
236	Lauraceae		

Table 4.2. Number trees and the elevation of transects.

	Number of trees	Elevation (m)	
		Start	Finish
Transect 1	236	328.27	415.14
Transect 2	106	165.81	258.17
Transect 3	170	441.05	384.96
Total	512		

Figure 4.1. Location of transects.



4.3. Results

4.3.1. Family diversity of transect trees

Table 4.1 lists all transect trees (n = 512), of which 99 were identified to species level, 19 to genus, 389 to family, and five unidentified. Ten trees were identified with a degree of uncertainty (*cf.*). A total of 31 tree families were identified.

Transect 1 contained trees of 26 families, two unidentified trees, and 74 trees were identified to genus or species level. The three dominant families accounted for 43.6% of the trees and included Dipterocarpaceae (20.3%), Euphorbiaceae (12.7%) and Myrtaceae (10.6%). Family diversity along this transect was 5.2 families per 100 m, and had trees of five families not recorded on the other transects, or one distinct family per 100 m.

Transect 2 contained trees belonging to 19 families, all trees were identified to at least family level, and 31 were identified to genus or species level. The three dominant families accounted for 61.3% of the trees and included Euphorbiaceae (32.1%), Anacardiaceae (18.9%) and Myrtaceae (10.3%). Diversity along this transect was 6.3 families per 100 m, and three families along this transect were not recorded along the other transects, or one distinct family per 100 m.

Transect 3 contained trees belonging to 22 families, three trees were unidentified, and 13 were identified to genus or species level. The three dominant families accounted for 45.8% of the trees and included Sapindaceae (18.2%), Euphorbiaceae (14.7%) and Myrtaceae (12.9%). Diversity along this transect was highest at 7.3 families per 100 m, and two families recorded along this transect were not recorded in the other transects, or 0.67 distinct families per 100 m.

When all trees are combined, the six most dominant families include Euphorbiaceae (17.4%), Myrtaceae (11.3%), Dipterocarpaceae (9.6%), Sapindaceae (8.4%), Anacardiaceae (6.8%) and Lauraceae (6.6%).

4.3.2. Height

Average height of all 512 transect trees was 9.34 ± 3.52 m, with 71% lower than 10 m, 21% between 10 and 14.9 m, and 8% above 15 m. Figure 4.2 illustrates transect tree heights. Transect 1 and 2 are similar except Transect 1 has trees in a taller height class which are absent from Transect 2. Almost all of these tall trees are from a single dipterocarp species: *Parashorea stellata* (white seraya). Both Transects 1 and 2 had a fairly healthy secondary canopy, an abundance of lianas and a more open understory than Transect 3. Descriptive data for height can be found in Table 4.3.

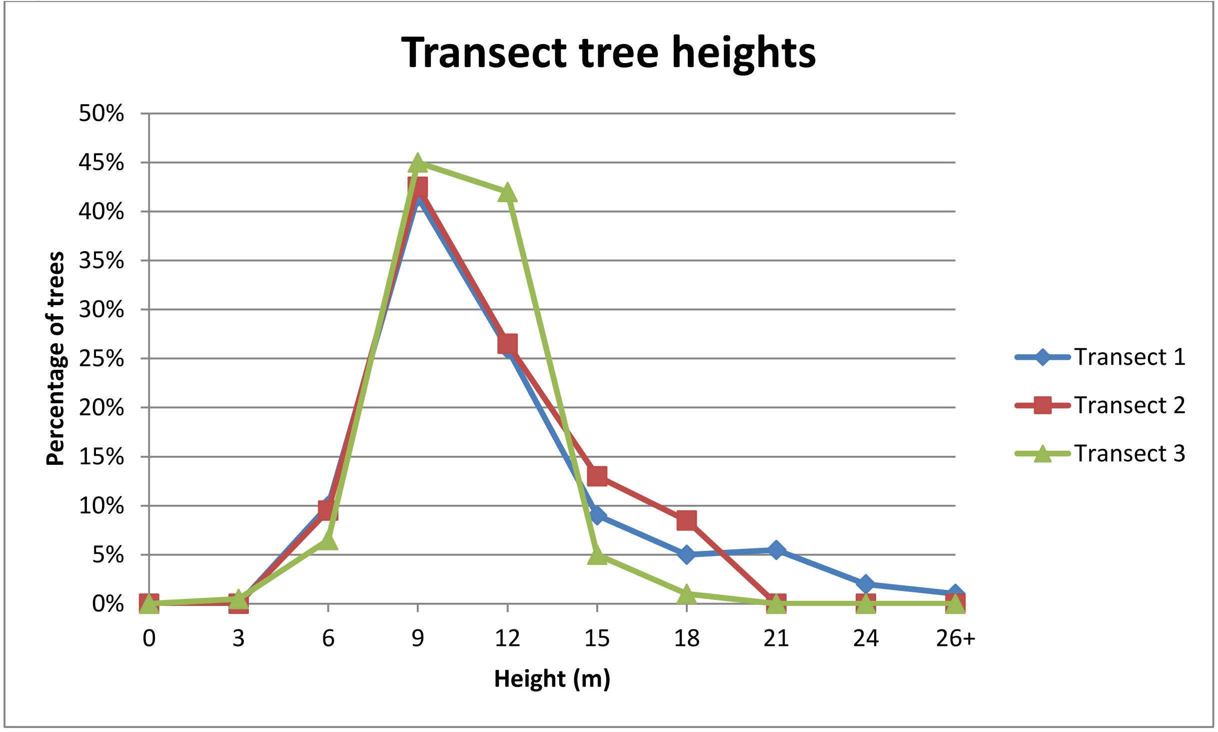
The tallest trees were found on Transect 1: average height of 9.8 ± 4.38 m. This was the only transect with trees higher than 17 m and contained the 21 highest transect trees, a majority of which were *Parashorea stellata*. Of the 236 trees along this transect, 68% were lower than 10 m, 19% were between 10 and 14.9 m, 8% between 15 and 19.9 m, and 5% above 20 m.

High trees were also found on Transect 2 but none were above 17 m. The average height was 9.32 ± 3.08 m. Of the 106 trees on this transect, 65% were lower than 10 m, 26.5% were between 10 and 15 m and 8.5% were above 15 m.

Transect 3 was located on the southern slope and as such was located in a reportedly more disturbed area (see Chapter 3). Trees on Transect 3 were the lowest with an average height of 8.71 ± 2.03 m and no tree higher than 15.2 m. Of the 170 trees along this transect, 79% were lower than 10 m, 19% were between 10 and 15 m and 1% above 15 m.

Transects tree heights were compared for significant differences using one-way ANOVA of natural log transformed values. There were no significant differences between transect tree heights.

Figure 4.2. Height of transect trees on a 3-m increment scale.



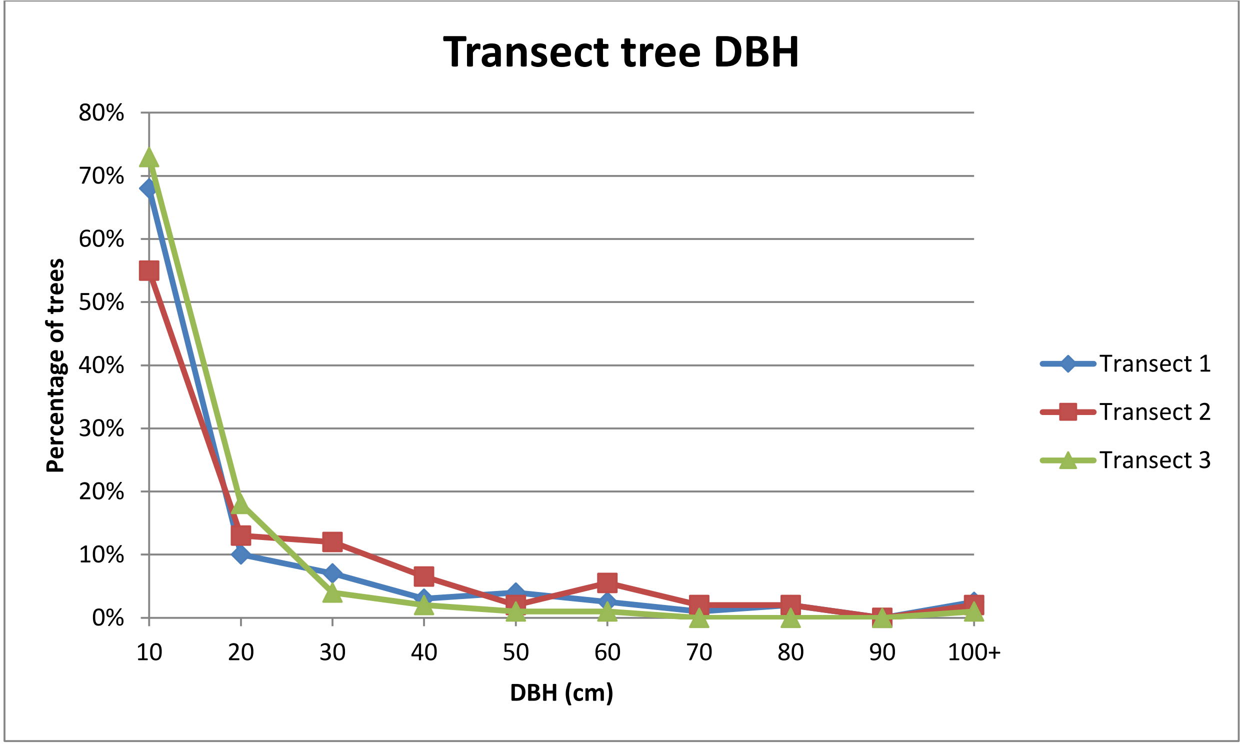
4.3.3. Diameter at breast height (DBH)

Combining all DBH data indicates that Son Tra is dominated by smaller (and most likely younger) trees: average DBH is 23.51 ± 23.24 cm. A majority (80%) measure below 30.0 cm DBH, 18% between 30.0 and 99.9 cm, and 2% measure 100.0 cm or greater. Figure 4.3 illustrates DBH and shows that Transect 1 and 2 have more trees with larger DBH than Transect 3. Descriptive data for DBH of each transect is shown in Table 4.3.

DBH of Transect 1 averaged 23.86 ± 22.77 cm. Of the 236 trees, 78% had a DBH between 10.0 and 29.9 cm, 20% had a DBH between 30.0 and 99.9 cm, and 2% had a DBH 100.0 cm or greater. DBH of Transect 2 averaged 27.90 ± 21.51 cm. Of the 106 trees, 68% were between 10.0 and 29.9 cm, 30% between 30.0 and 99.9 cm, and 2% had a DBH of 100.0 cm or greater. DBH of Transect 3 averaged 20.30 ± 24.70 cm. Of the 170 trees, 91% were between 10.0 and 29.9 cm, 8% were between 30.0 and 99.9 cm, and 1% had a DBH of 100.0 cm or greater. This transect contained the tree with the largest DBH of any transect tree with 233.7 cm. The tree was identified as a Moraceae.

Transects were compared for significant differences using one-way ANOVA of natural log transformed values. Results showed a significant difference between transect DBH (F (2, 509) = 6.999, p = 0.001). The Scheffé Least Significant Difference post- hoc test was applied revealing the significant difference was only between Transect 2 and Transect 3.

Figure 4.3. DBH of transect trees on a 10-cm incremental scale.



4.3.4. Crown width

The average crown width of all transect trees was 5.77 ± 2.90 m, and 91% had a crown width less than 10 m. Figure 4.4 illustrates transect crown width on a 5 m incremental scale showing that trees of Transect 1 and Transect 2 have larger crown widths than Transect 3, and

Transect 2 has more trees with a crown width around 10 m. Descriptive data is presented in Table 4.3

Transect 1 trees had an average crown width of 5.84 ± 3.40 m, and 87% of the trees had a crown width less than 10 m. Transect 2 trees had an average crown width of 6.63 ± 3.02 m, and 86% of the trees had a crown width less than 10 m. Transect 3 had an average crown width of 5.14 ± 1.69 m, and 99% of the trees had a crown width less than 10 m.

Crown width was compared for significant differences between transects using one-way ANOVA of natural log transformed values. Results showed a significant difference between transect crown widths (F (2, 509) = 7.767, p = 0.0005). Scheffé Least Significant Difference post- hoc test was applied revealing the significant differences were between Transect 1 and Transect 2, and between Transect 2 and Transect 3 indicating that crown width of trees along Transect 2 were significantly wider compared to the other transects.

Figure 4.4. Crown width of transect trees.

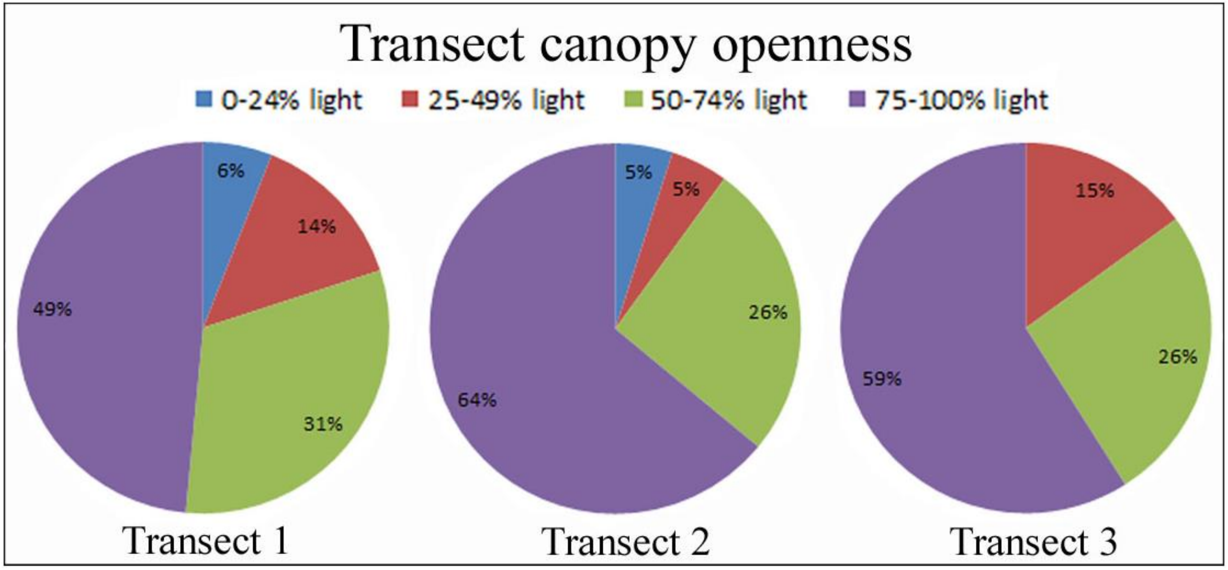
4.3.5. Canopy density

Light coming through the canopy was measured every 5 m along each transect. To briefly review the scale described in Chapter 3, a measure of 0% was used to indicate no sky was visible and the canopy was entirely closed, and a measure of 100% indicated entirely open sky and no canopy cover.

Transect 1 included 101 points with a mean of 65.8% ± 22.0 % light, and had the densest canopy with 20% of the points measuring light below 50%, and 48% of the points measuring light above 75%. Transect 2 included 61 points with a mean of 73.2% ± 21.0% light, had 10% of the points measuring light below 50%, and 64% of the points measuring light above 75%. Transect 3 included 61 points with a mean of 72.1% ± 17.9% light, had 15% of the points measuring light below 50%, and 59% of the points measuring light above 75%.

Figure 4.5 illustrates the percentages of light and therefore density of the canopy on each transect. Descriptive canopy data is provided in Table 4.3.

Figure 4.5. Canopy density of transects



4.3.6. Stand basal area (SBA) and density

Stand basal area is the surface area of all tree trunks with a DBH of 10 cm or greater per ha of forest. This is useful in describing stand competition (Reid & Stephen, 2001), which is the competition between individuals, species or groupings of species for resources such as water, sunlight and nutrients (additionally see Callaway & Walker, 1997; Castagneri et al., 2012; Haijin Shi & Lianjun Zhang, 2003; Kocher & Harris, 2007; Perry, 1985; Simard & Durall, 2004). Because transect trees were only identified to family level, SBA is presented here as the combination of all trees on a transect (*i.e.*, it is not species specific). Transect 1 had a SBA of 50.4 m^2/ha, Transect 2 was 43.1 m^2/ha, and Transect 3 was 56.9 m^2/ha. Competition between trees is therefore greatest on Transect 3 and weakest on Transect 2, which partly explains why trees are significantly wider on this transect. Transect SBA values are presented in Table 4.3.

Density is another measure to describe the degree of tree competition, with greater density indicating greater competition. Transect 1 had a tree density of 590 trees/ha, Transect 2 had 441.67 trees/ha, and Transect 3 had 708.34 trees/ha. As with SBA, density measurements illustrate competition was greatest on Transect 3 and weakest on Transect 2. The inclusion of lianas in future transects may provide additional insights into stand competition on Son Tra (see Perez-Calicrup & Barker, 2000). Transect density values are presented in Table 4.3.

4.3.7. Tree mortality

During the 13 consecutive months of tree phenology analysis, 15 trees were recorded as dead. Four of these trees were dead when the transects were established (they were still recorded in transect data due to my initial uncertainty if they were alive or dead), one died as a result of being uprooted from a large fallen branch, seven died from unknown causes, and three trees were dying towards the end of the study (noted as the dying of all mature and young leaves and lack of leaf replacement over one month). One tree was cut down, but is not considered a mortality as the trunk was still alive. Of all transect trees, 2.9% died. Of these, 12 died on Transect 1 (5.1% of Transect 1 trees), two died on Transect 2 (1.9%) and one on Transect 3 (0.6%). This equals to 15 natural deaths per 0.88 ha in 13 months, or about 16 trees/ha/year. The height of dead trees ranged from 3.3 to 14 m with a mean of 8.3 m. It is not clear why the highest tree mortality occurred on Transect 1. The only trees noted as dead during transect establishment (n=4) were on Transect 1, which inflates this mortality percent. Most dead trees were low in height, and Transect 1 had the highest trees and the densest canopy with the least amount of light reaching the understory. This may also have contributed to the increased tree mortality along Transect 1. Table 4.3 includes descriptive data for tree mortality.

Table 4.3. Transect characteristics.

Transect	Height (m)	Crown width (m)	DBH (cm)	SBA (m^2/ha)	Density (trees/ha)	Canopy density (%)	Mortality (%)
1	9.8 ± 4.4	5.8 ± 3.4	23.9 ± 22.8	50.4	590.0	65.8 ± 22.0	5.1%
2	9.3 ± 3.1	6.6 ± 3.0	27.9 ± 21.6	43.1	441.67	73.2 ± 21.0	1.9%
3	8.7 ± 2.0	5.1 ± 1.7	20.3 ± 24.8	56.9	708.34	72.1 ± 17.9	0.6%

4.3.8. Forest productivity

The following reports on phenophase patterns compares these patterns between seasons, transects and with weather cycles established in Chapter 3. As a reminder, the dry season is from February through May, and the wet season is from June through January. Methods used to record phenophase data were presented in Chapter 3.

4.3.8.1. Leaf flush

Evaluating all transect data, the monthly average percentage of trees with any amount of leaf flush was considerably high: 93.06 ± 11.32%. However, during the majority of months trees with leaf flush contained between 1% and 24.9% leaf flush in their canopy (category 1), and if only categories 2 (25% to 49.9%), 3 (50% to 74.9%), and 4 (75% to 100%) are considered, the monthly average percentage of trees with leaf flush is 4.53 ± 4.48% trees. Figure 4.6 combines transect monthly averages over the duration of the study showing trees with any amount of leaf flush (categories 1 through 4) and trees with 25% or greater leaf flush (categories 2 through 4). The figure shows there were peaks in flush at the end of the dry season and beginning of the wet season from April through August, but young leaves were available throughout the year. During the time of peak leaf flush, there are generally less trees with leaf flush. The months with the greatest peaks in leaf flush were May and June (11.50% and 11.63%). During the wet season, 92.82% of all trees had leaf flush, and 3.79% had 25% or greater leaf flush. During the dry season 93.56% of all trees had leaf flush, and 5.43% had 25% or greater leaf flush. Testing these findings for significance using the two proportion z-test confirmed that the seasons are not significantly different, and this is partly attributed to new leaf flush peaking during the end of the dry season and beginning of the wet season.

Leaf flush patterns of each transect is shown in Figure 4.7, illustrating that all transects are similar concerning leaf flushing. Testing for significant differences between transect trees with leaf flush (at 25% or greater leaf flush) using the three independent-group proportion z-test revealed no significant differences between transects.

Leaf flush was widely available throughout the year in small quantities. Therefore leaf flush of 25% or greater is a better indication of annual trends in leaf flushing and availability. Figure 4.8 shows all transect trees with 25% or greater leaf flush in comparison to temperature data. Using Pearson’s Correlation coefficient, there was a significant positive correlation between these two variables (r (10) = 0.71, p = 0.009). A correlation between leaf flush and monthly precipitation (Figure 4.9) was not significantly different, similar to other studies (see Ha Thang Long, 2009; Rawson, 2009).

Figure 4.6. Leaf flush phenology patterns (dry season is February through May).

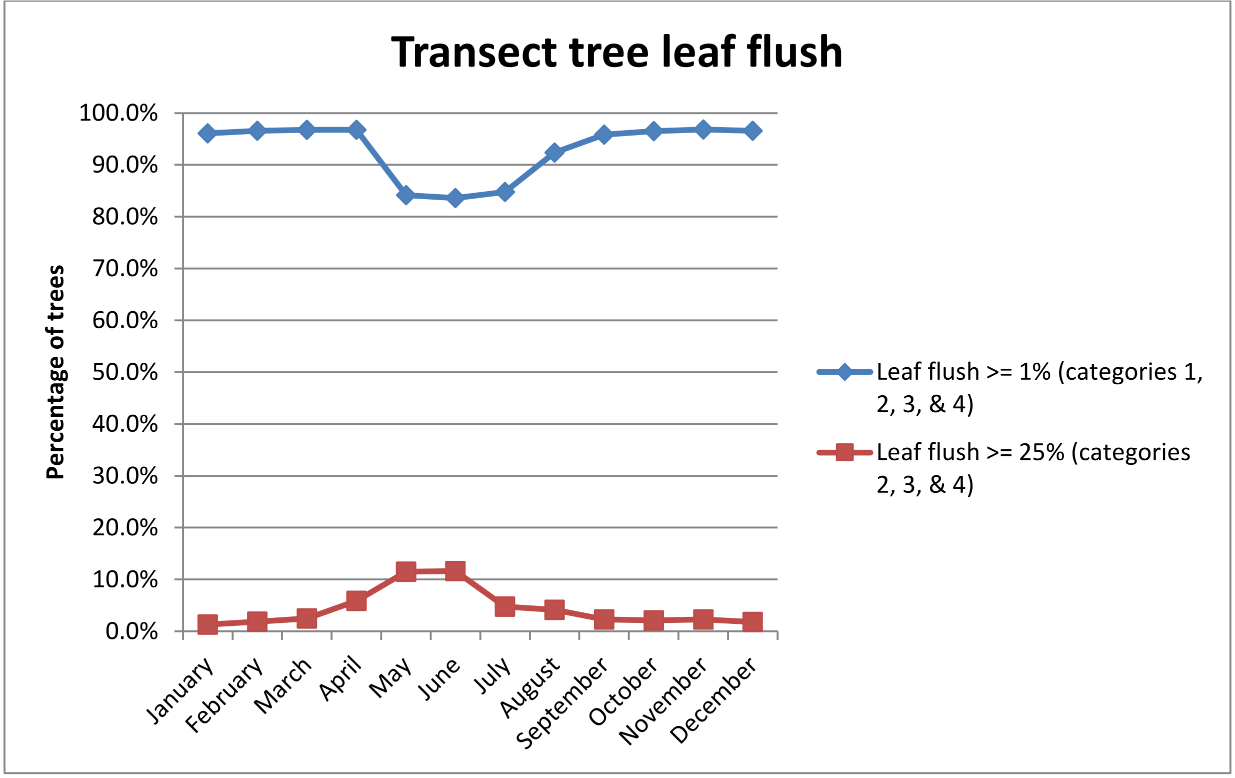


Figure 4.7. Comparing leaf flush percentages between transects.

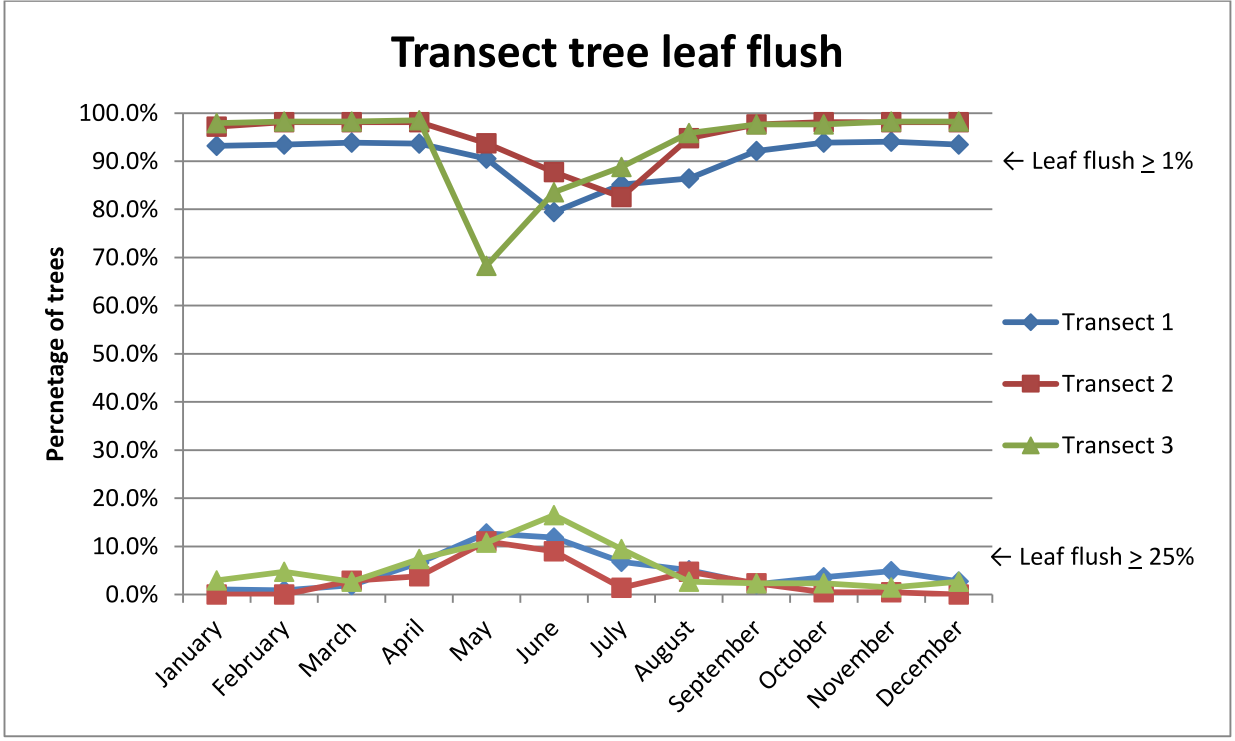


Figure 4.8. Leaf flush and temperature (dry season is February through May).

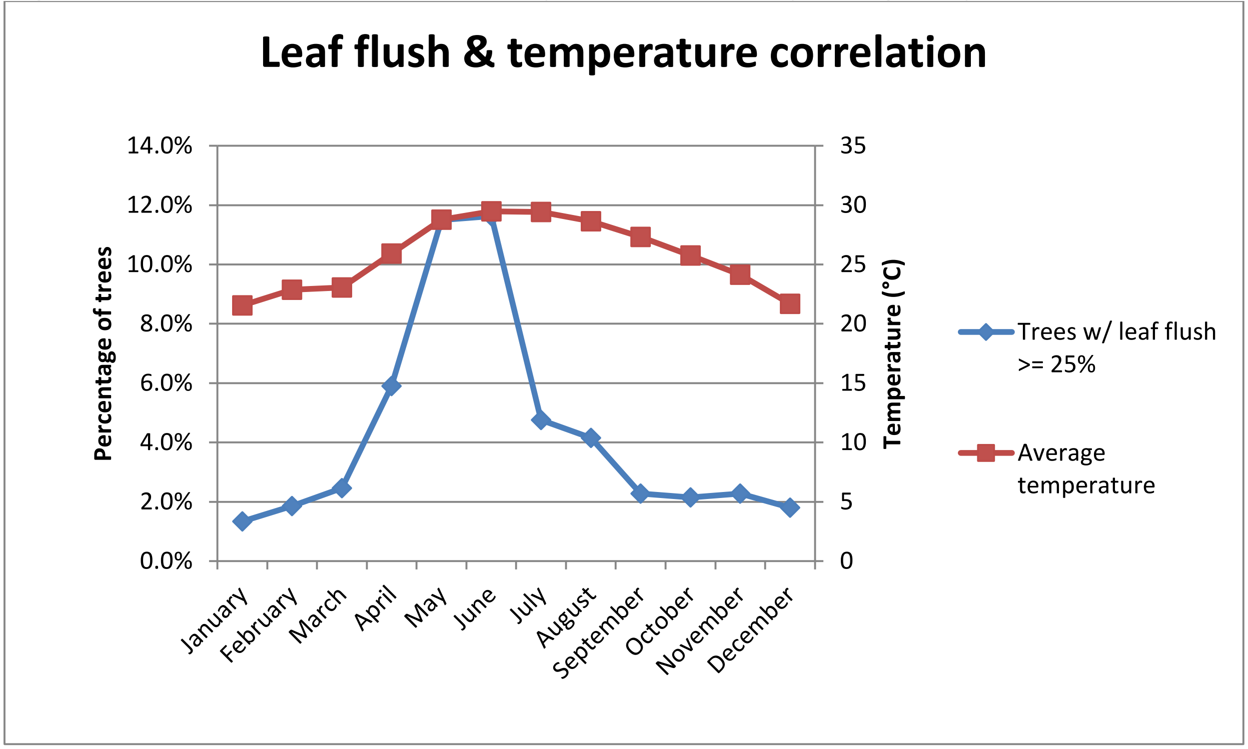
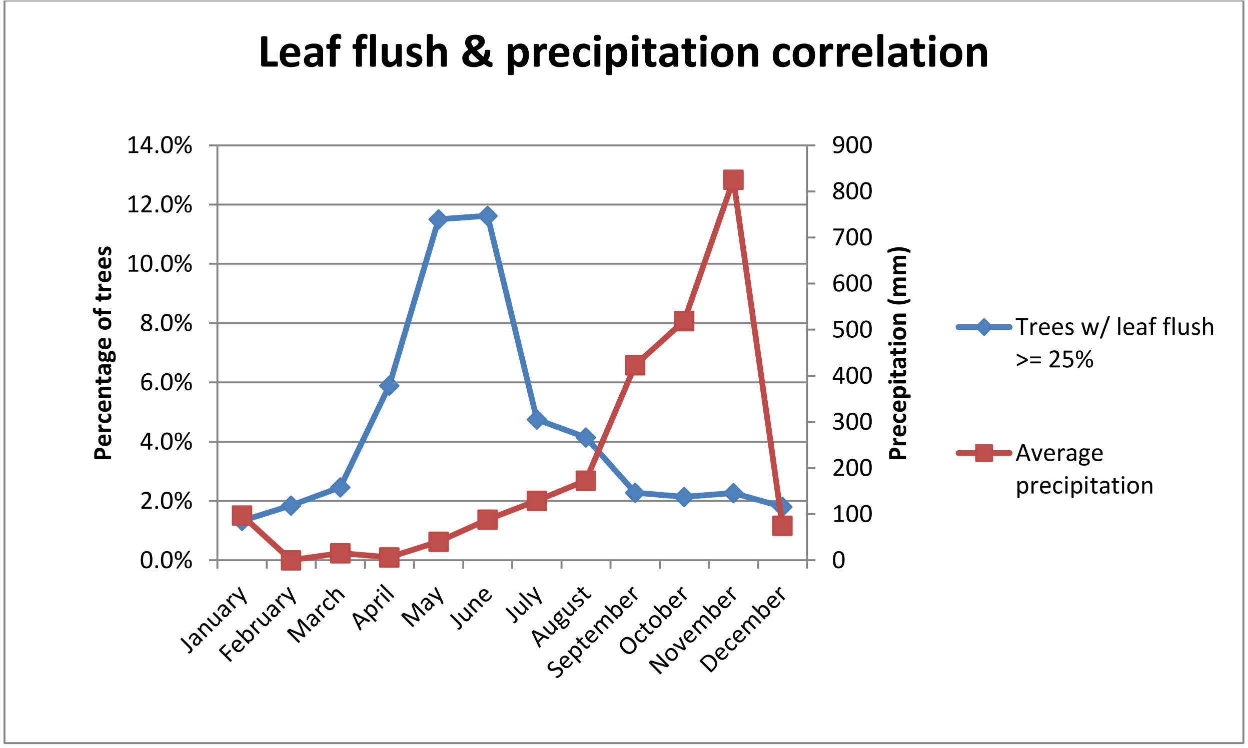


Figure 4.9. Leaf flush and precipitation (dry season is February through May).



4.3.8.2. Leaf fall/dead leaves

Evaluating all transect data, the monthly average percentage of trees with dead leaves was low: 8.55 ± 12.45%. In the majority of trees with leaf fall, the percentage of dead leaves is less than 25%, and if only categories 2, 3, and 4 (from 25% to 100% dead leaves) are considered, then the monthly average is 0.71 ± 0.74%. Figure 4.10 combines monthly averages of all transect trees with any percentage of dead leaves and monthly averages of trees with 25% or greater dead leaves. It shows a peak in deciduousness during the dry season from February through May. Combining all transects, 22.17% of the trees had dead leaves during the dry season and only 0.38% had dead leaves during the wet season. Testing for significant differences between seasons using the two proportion z-test supports deciduous seasonality ($z = 33.35$, $p <= 0.0001$).

Leaf fall patterns of each transect are shown in Figure 4.11. Each transect had a distinct peak in leaf fall during the dry season. Comparing transect leaf fall using the three independent-group proportion z-test revealed no significant differences in the average number of trees with leaf fall between transects.

Because few trees shed more than 25% of their leaves during a single record, the best indicator of leaf fall is 1% or greater leaf fall, which is compared to weather patterns in Figures 4.12 and 4.13. Leaf fall occurs in concert with the dry season months, which is when the average temperature was rising (Figure 4.12), but when precipitation was lowest (Figure 4.13). Using Pearson's Correlation coefficient, leaf fall and temperature, and leaf fall and precipitation, were not significantly correlated. Although not significant, the correlation between leaf fall and precipitation is strong and negative ($r(9) = -0.57$, $p = 0.06$), indicating that leaf fall tends to occur when precipitation is low.

Figure 4.10. Leaf fall (dry season is February through May).

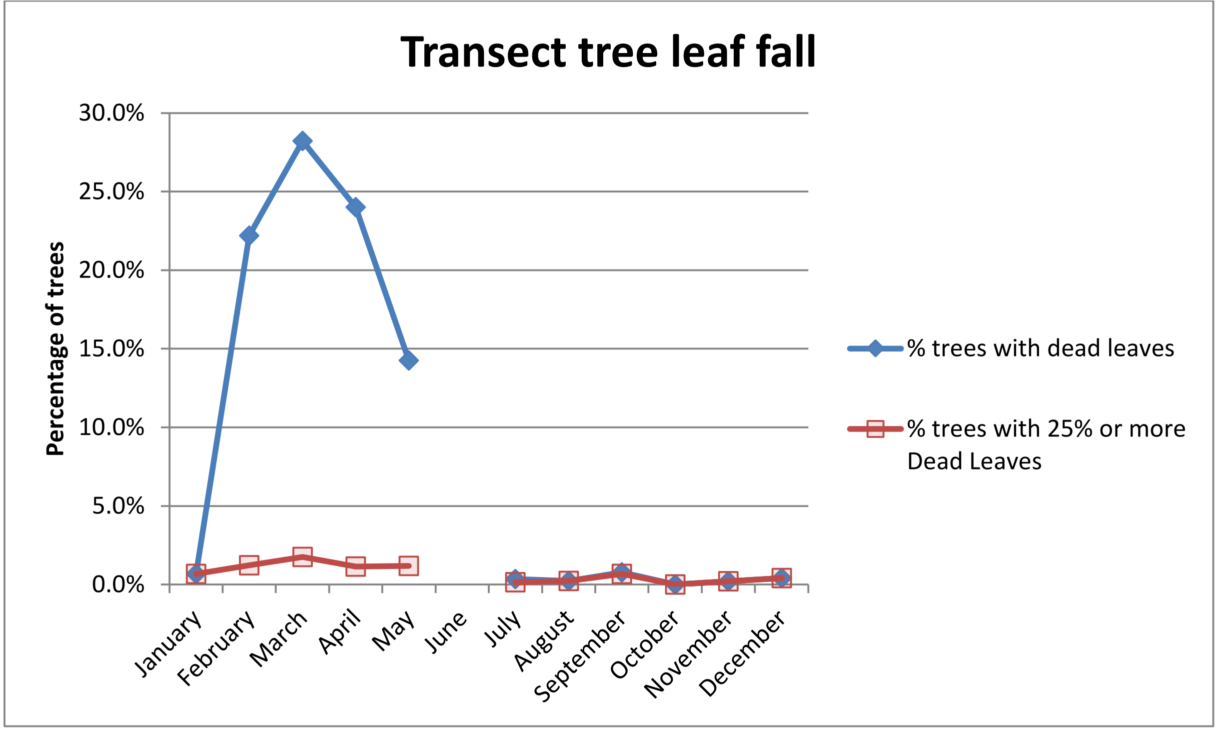


Figure 4.11. Leaf fall between transects.

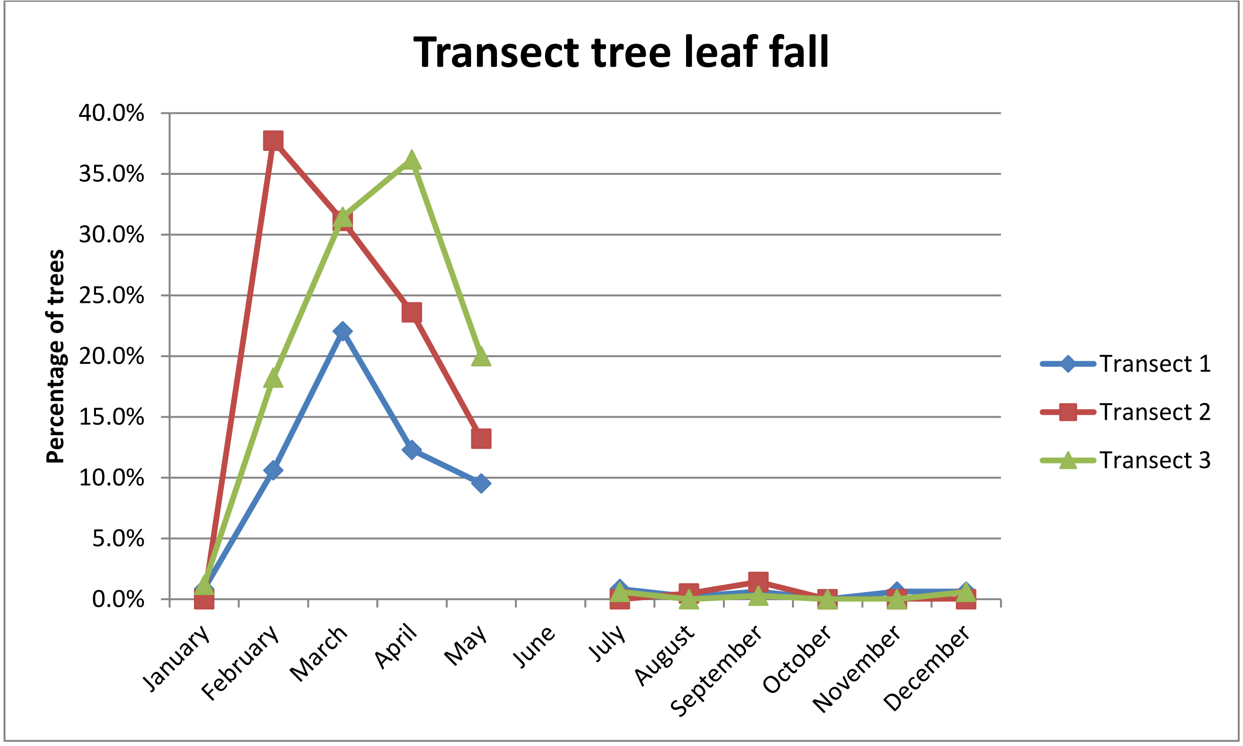


Figure 4.12. Leaf fall and temperature (dry season is February through May).

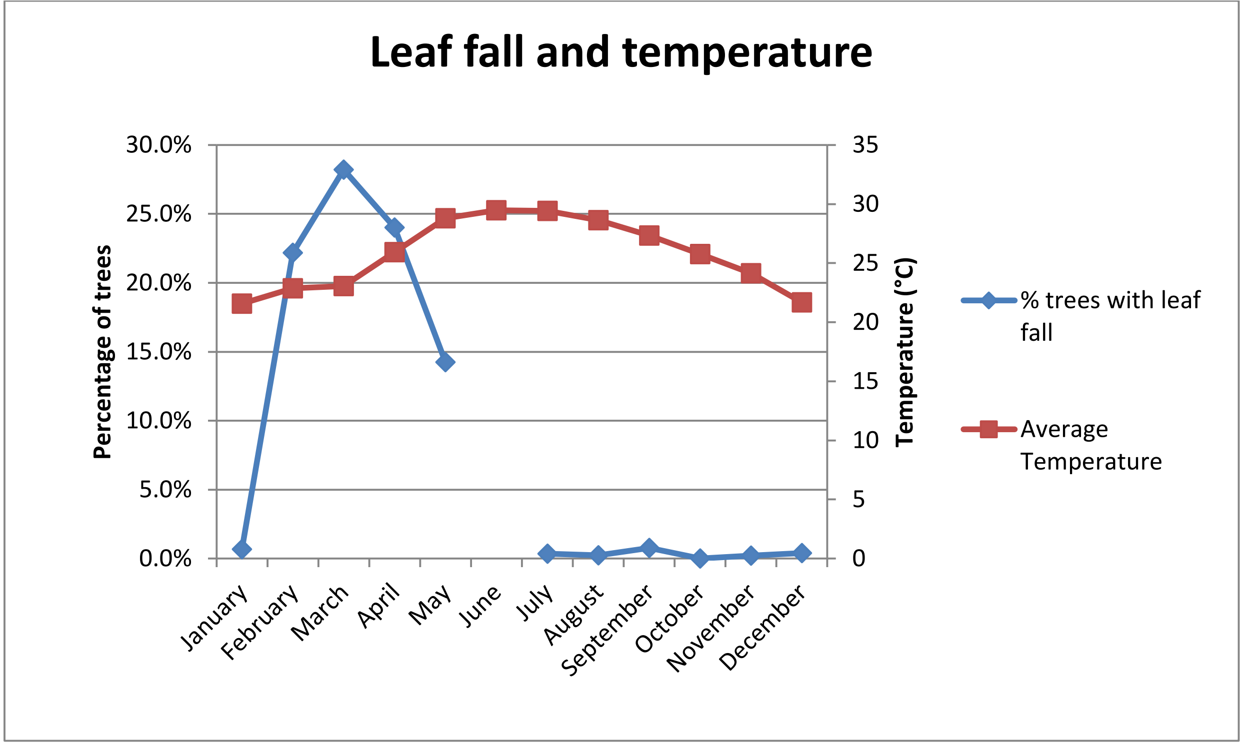
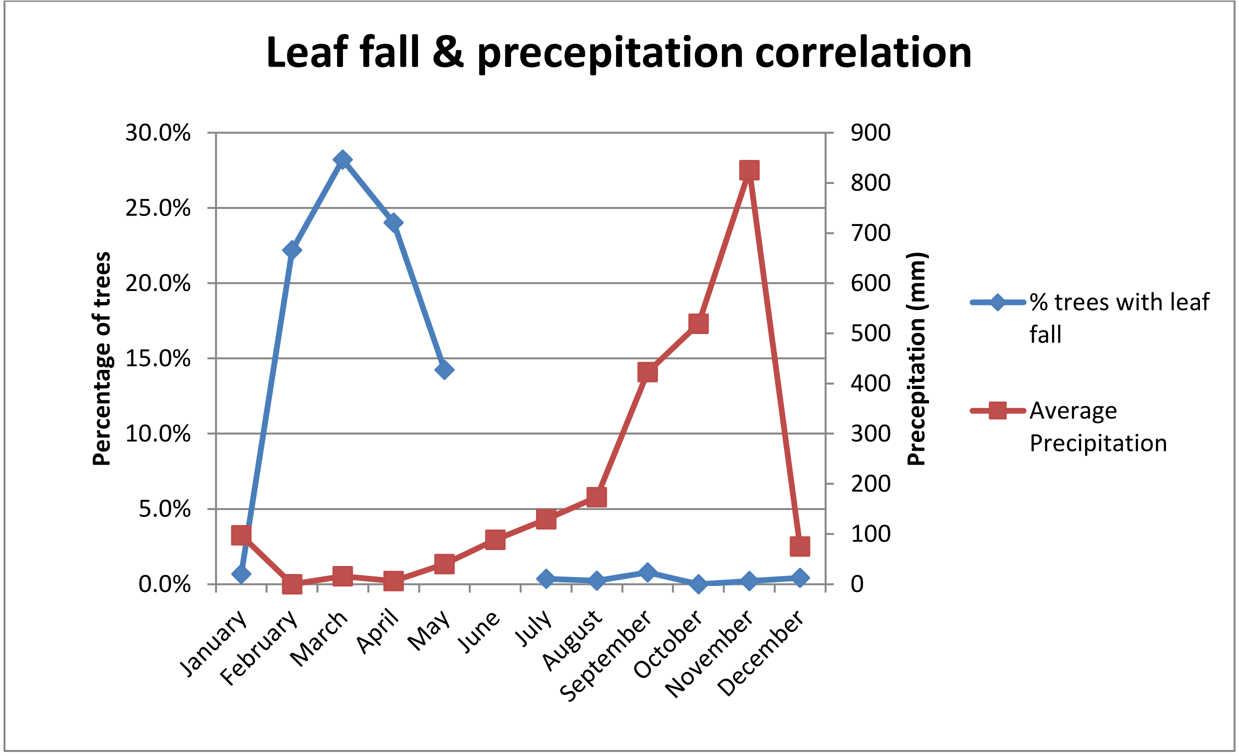


Figure 4.13. Leaf fall and precipitation (dry season is February through May).



4.3.8.3. Flowering

Evaluating all transect data, the monthly average percentage of trees flowering was 8.97 ± 6.27%. Most of these flowering trees had less than 25% of their canopy flowering (category 1). If only categories 2, 3, and 4 are considered, the monthly average of trees flowering was 2.33 ± 2.78%. Figure 4.14 combines transect monthly averages indicating a flowering peak during the dry season and extending into the early wet season, similar to the pattern observed for leaf flush. There are two peaks in flowering; a primary peak during the dry season and a secondary peak during the early wet season. Dry season months average 12.5% trees flowering per month, and the wet season averages 6.7% trees flowering per month. Testing for significant differences using the two proportion z-test indicates significant flowering seasonality, peaking during the dry season ($z = 10.17$, $p <= 0.0001$).

Flowering patterns for each transect are shown in Figure 4.15 for trees with 1% of their canopy or greater flowering. Transect 1 and 2 show a bimodal peak in flowering from March through August during the dry season to early wet season, with the first peak around March and the second around August. Transect 3 has a less defined flowering season from March through November (mid-dry season through the mid-wet season) and although there are peaks similar to the other transects these are less defined. The three independent-group proportion z-test revealed no significant differences in the annual percentage of trees flowering between transects. Testing each transect independently for seasonal differencing in trees flowering revealed all transects flower significantly more during the dry season: Transect 1 ($z = 8.13$, $p <= 0.0001$), Transect 2 ($z = 7.49$, $p <= 0.0001$), and Transect 3 ($z = 2.86$, $p = 0.004$). This indicates that the dry season is the primary flowering peak for all transects.

The primary flowering peak occurs when temperatures are transitioning from low to high (Figure 4.16) and when precipitation is lowest (Figure 4.17). The secondary peak occurs when temperature and precipitation are high. Using Pearson's Correlation coefficient, flowering and temperature, and flowering and precipitation, were not significantly correlated.

Figure 4.14. Flowering (dry season is February through May).

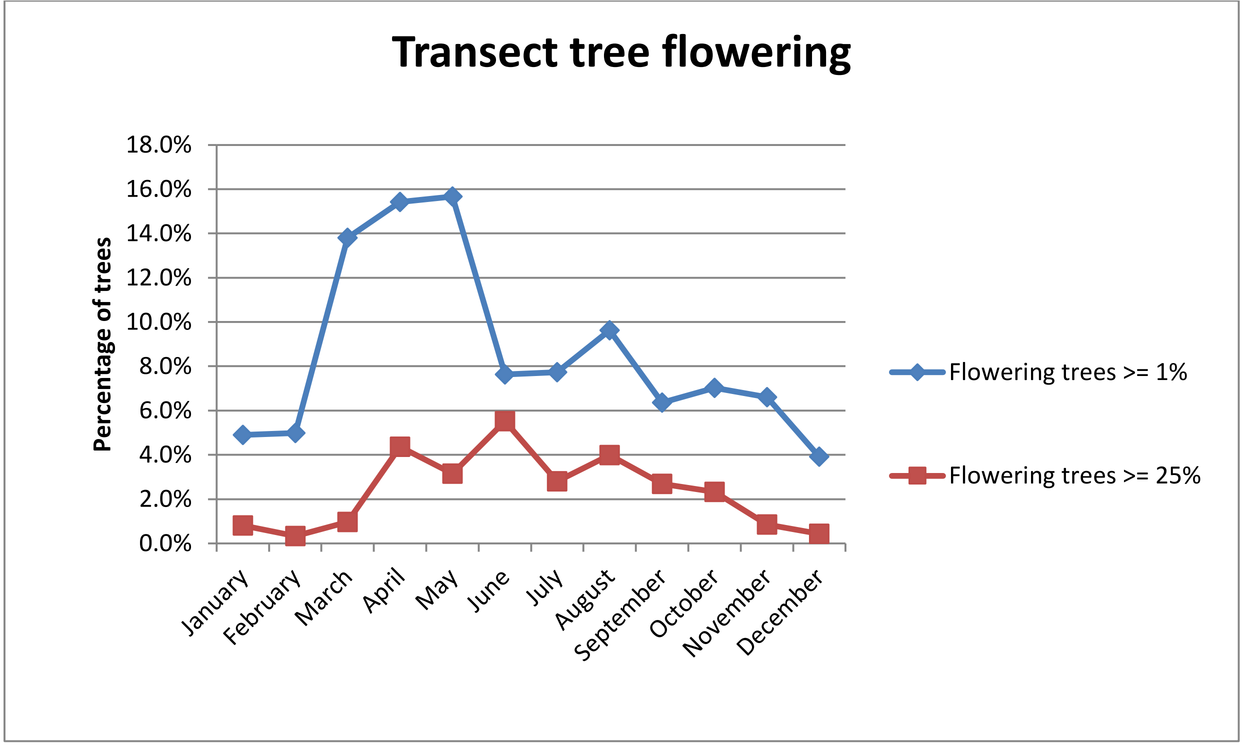


Figure 4.15. Flowering patterns between transects.

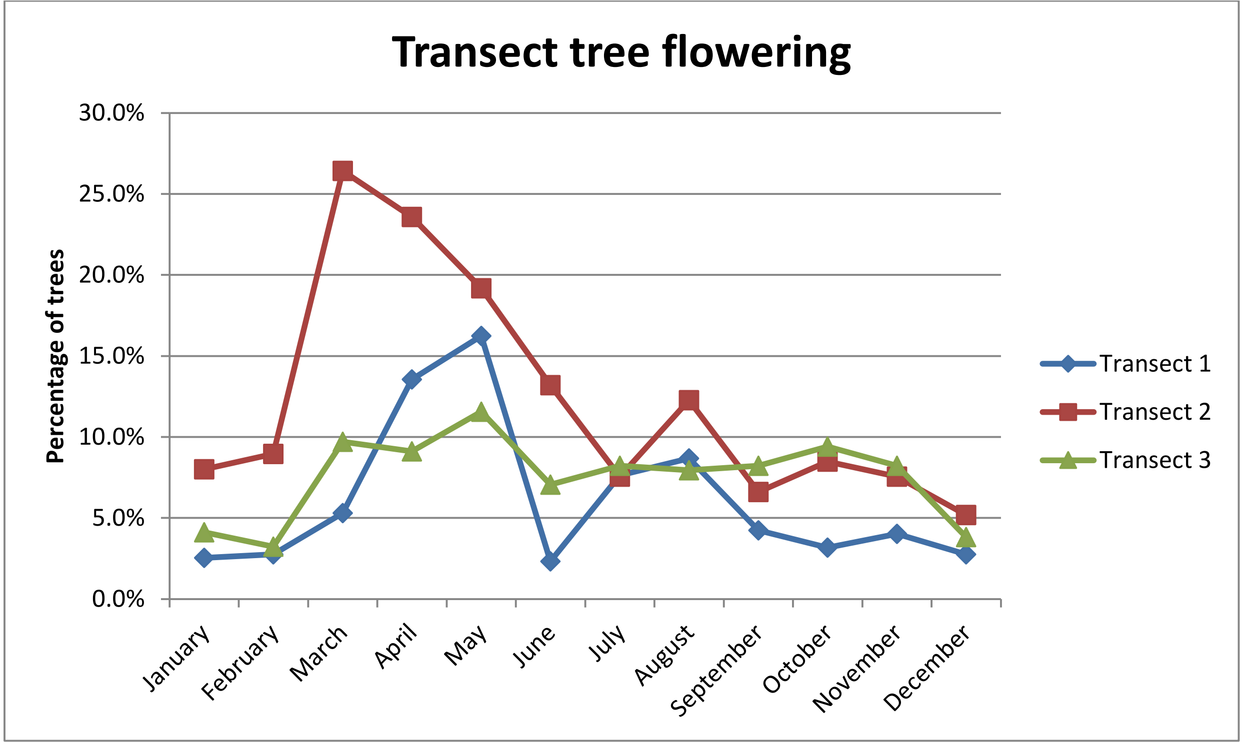


Figure 4.16. Flowering and temperature (dry season is February through May).

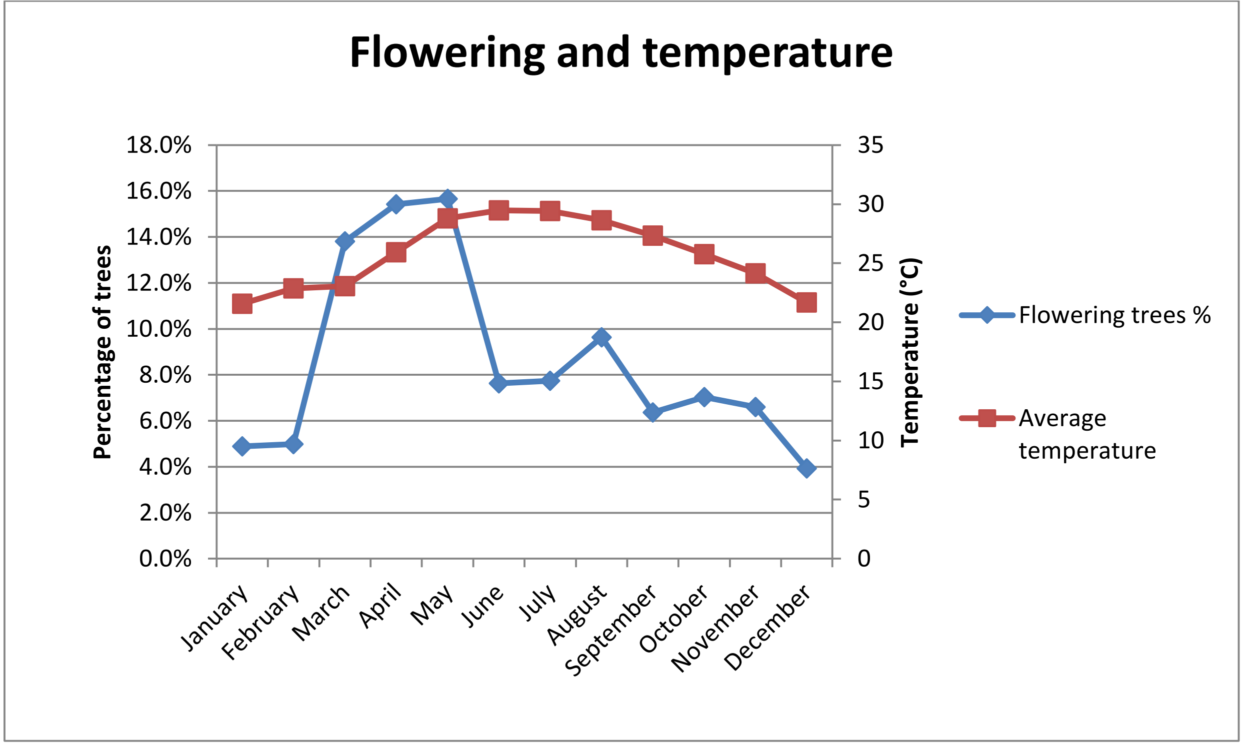
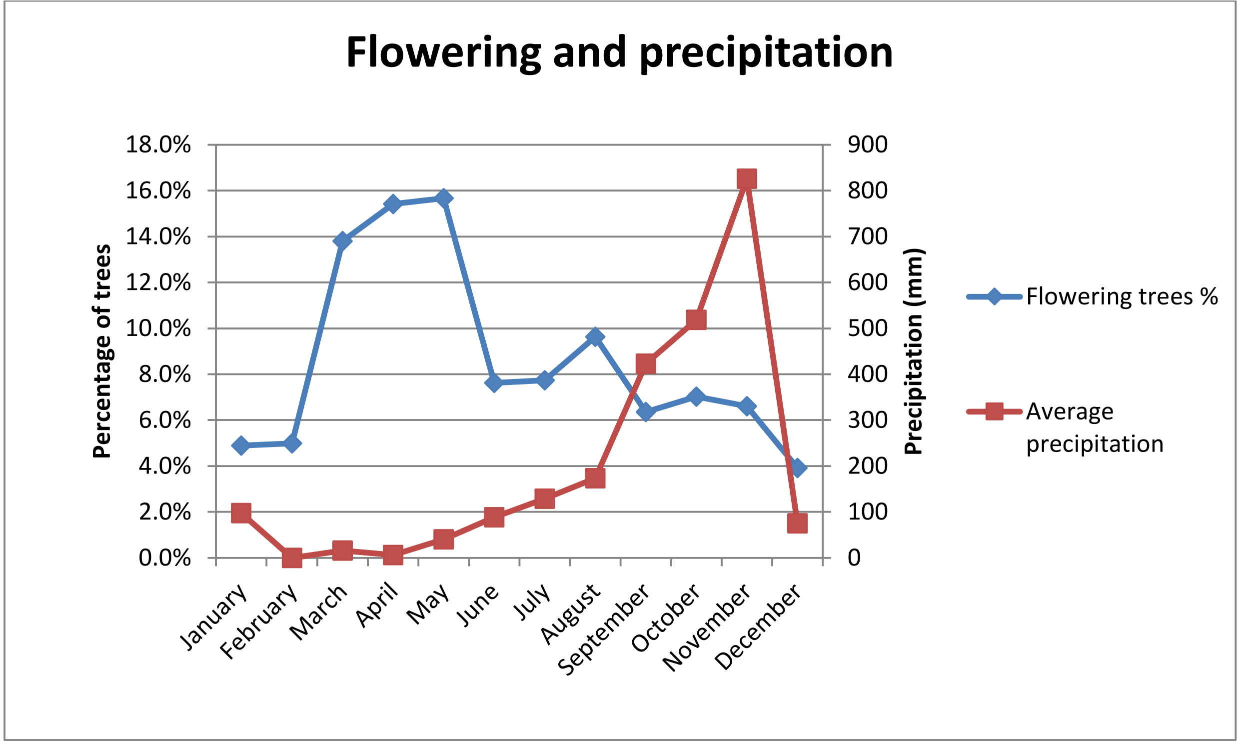


Figure 4.17. Flowering and precipitation (dry season is February through May).



4.3.8.4. Fruiting

Evaluating all transect data, the monthly average percentage of fruiting in all transect trees was 3.66 + 2.22%. Most of these fruiting trees had less than 25% of their canopy fruiting (category 1). If only fruiting above 25% (categories 2, 3, and 4) are considered then the monthly average was 0.57 + 1.14% trees. Figure 4.18 combines transect monthly averages showing the percentage of fruiting trees at 1% and greater and 25% and greater fruits, and indicates a strong peak in fruiting towards the end of the wet season in November when the majority of observed fruiting trees bore fruit. There was a comparable peak in fruiting at the beginning of the wet season following the primary flowering peak. This peak has fewer trees fruiting, but of those they did so in greater quantities. Seasonally the dry season had 2.81% trees fruiting and the wet season had 4.04% trees fruiting on average per month. Testing for significant differences using the two proportion z-test indicates significantly more fruiting during the wet season (z = 3.71, p = 0.0002), which is most similar to wet tropical forests as opposed to dry tropical forests.

Fruiting patterns of each transect are shown in Figure 4.19, comparing all trees bearing 1% or greater fruits. Transect 2 is the only transect with a primary fruiting peak in the dry season (May). Transect 3 has a primary fruiting peak after the onset of the wet season (July). Transect 1 and Transect 2 each had a short fruiting peak early in the wet season (August). All three transects had a fruiting peak late in the wet season (November), following the late wet season flowering peak. For Transect 1 this is the more significant peak. Figure 4.18 suggests that the late wet season fruiting peak is more significant than the peak at the end of the dry season and beginning of the wet season. However, as is apparent in Figure 4.19 the timing of the first peak is different between transects, and therefore monthly averages are lower compared to the more similarly timed fruiting peak in November. The three independent-group proportion z-test revealed no significant differences in the percentage of fruiting trees between transects.

Using Pearson's Correlation coefficient, fruiting and temperature were not significantly correlated. However, fruiting and precipitation were significantly and positively correlated (r (10) = 0.68, p = 0.02), indicating fruiting is timed to increases in precipitation.

Figure 4.18. Fruiting (dry season is February through May).

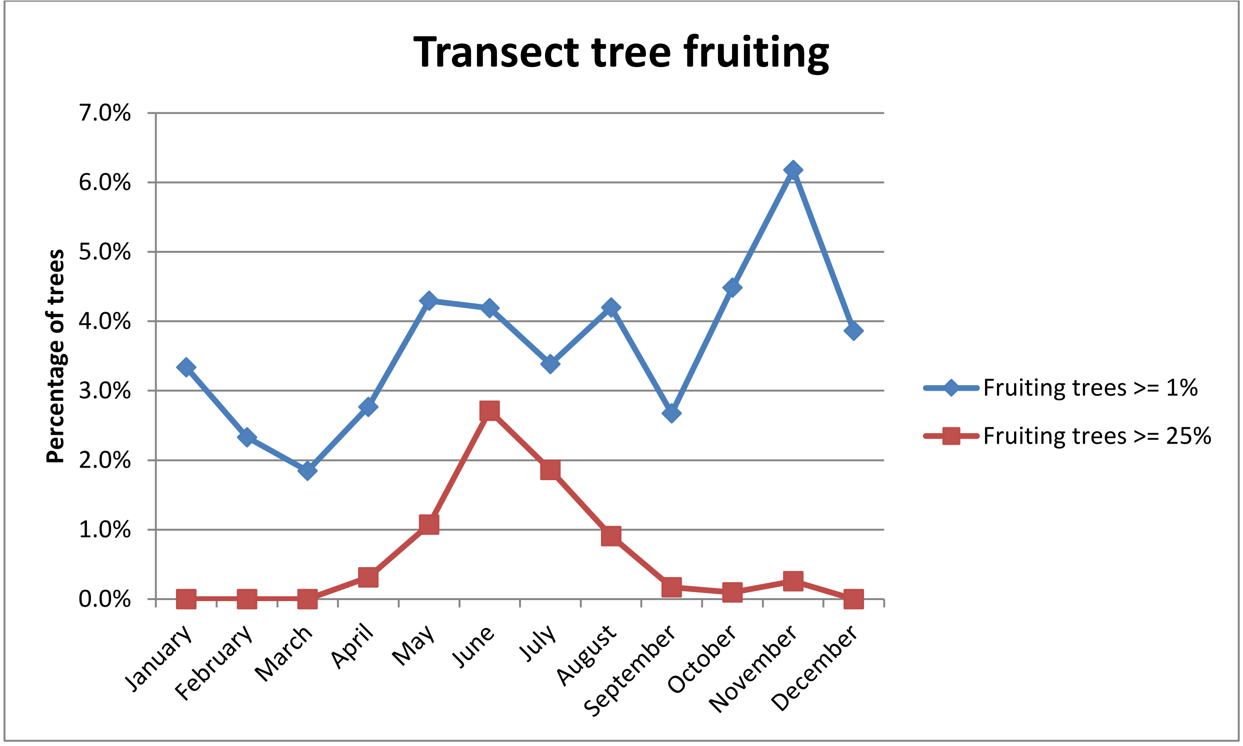


Figure 4.19. Fruiting patterns between transects.

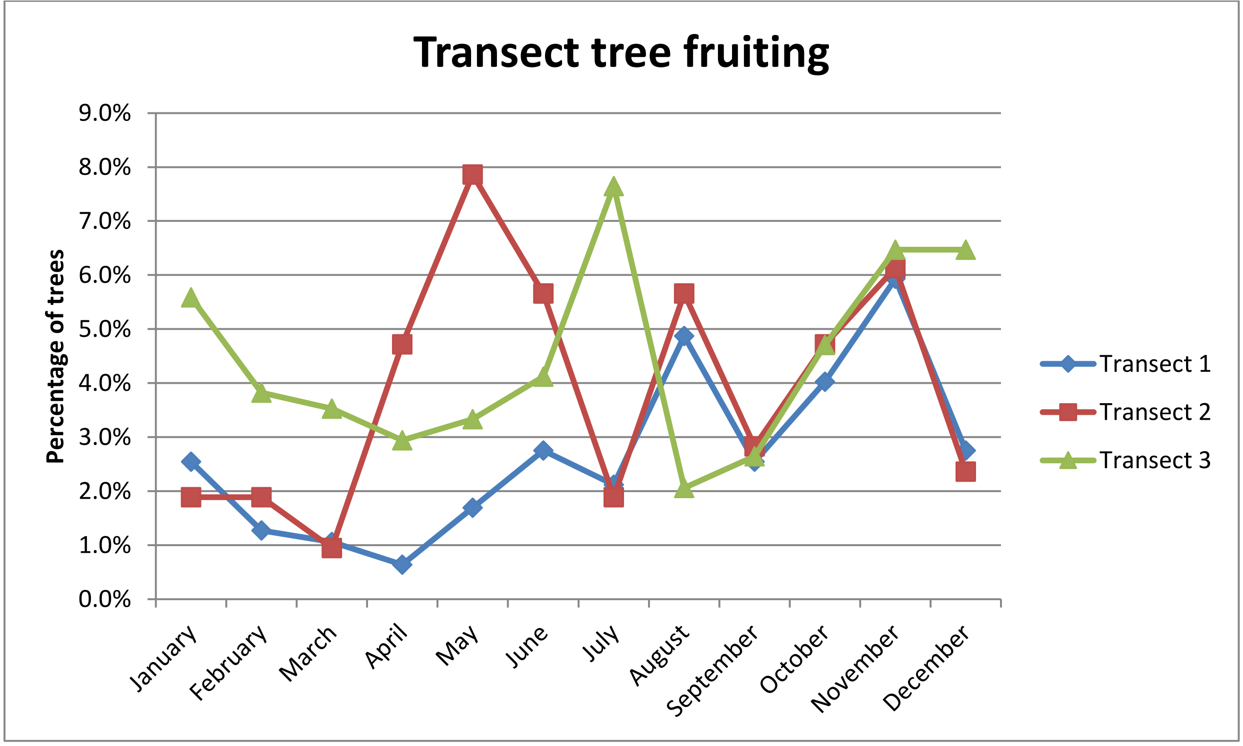


Figure 4.20. Fruiting and temperature (dry season is February through May).

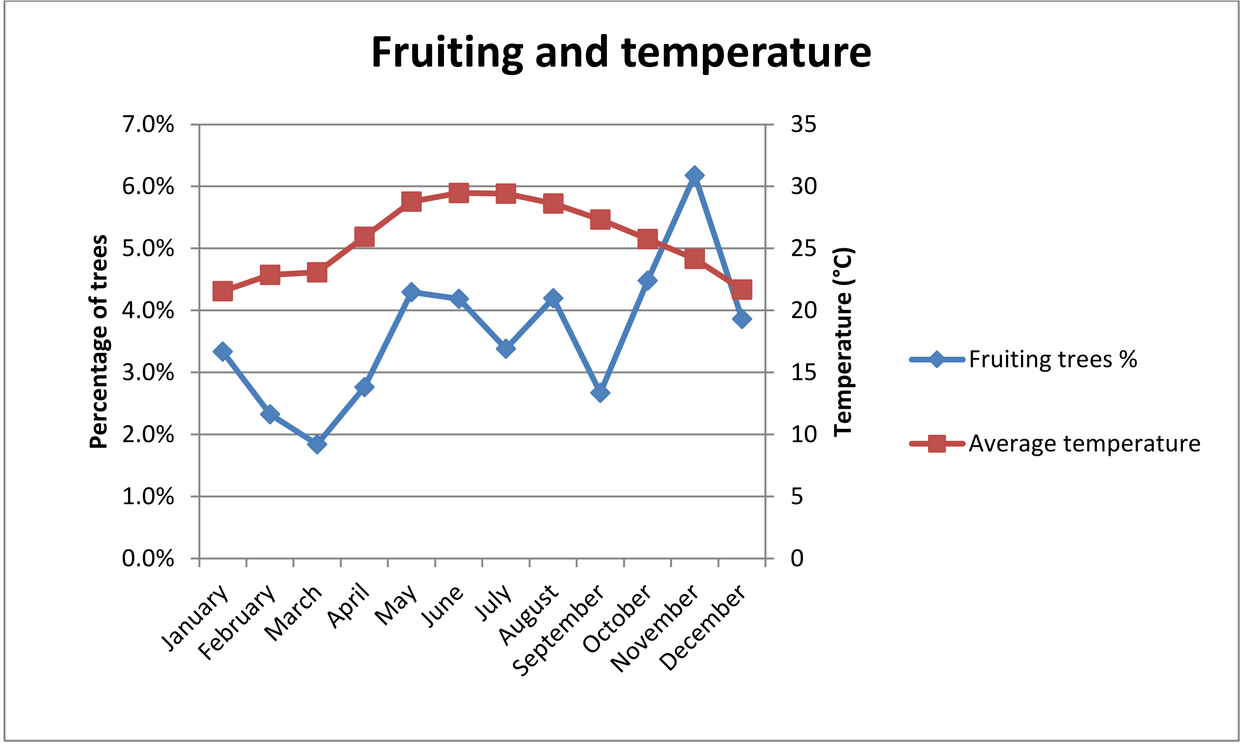
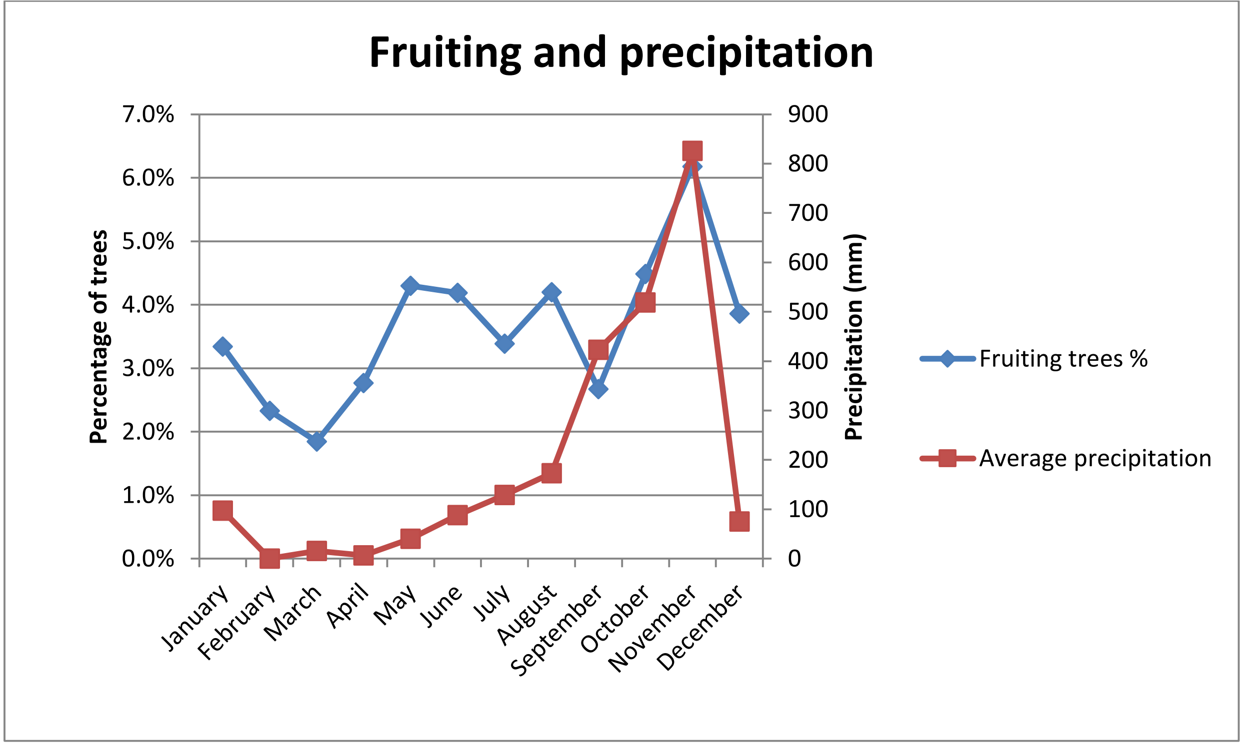


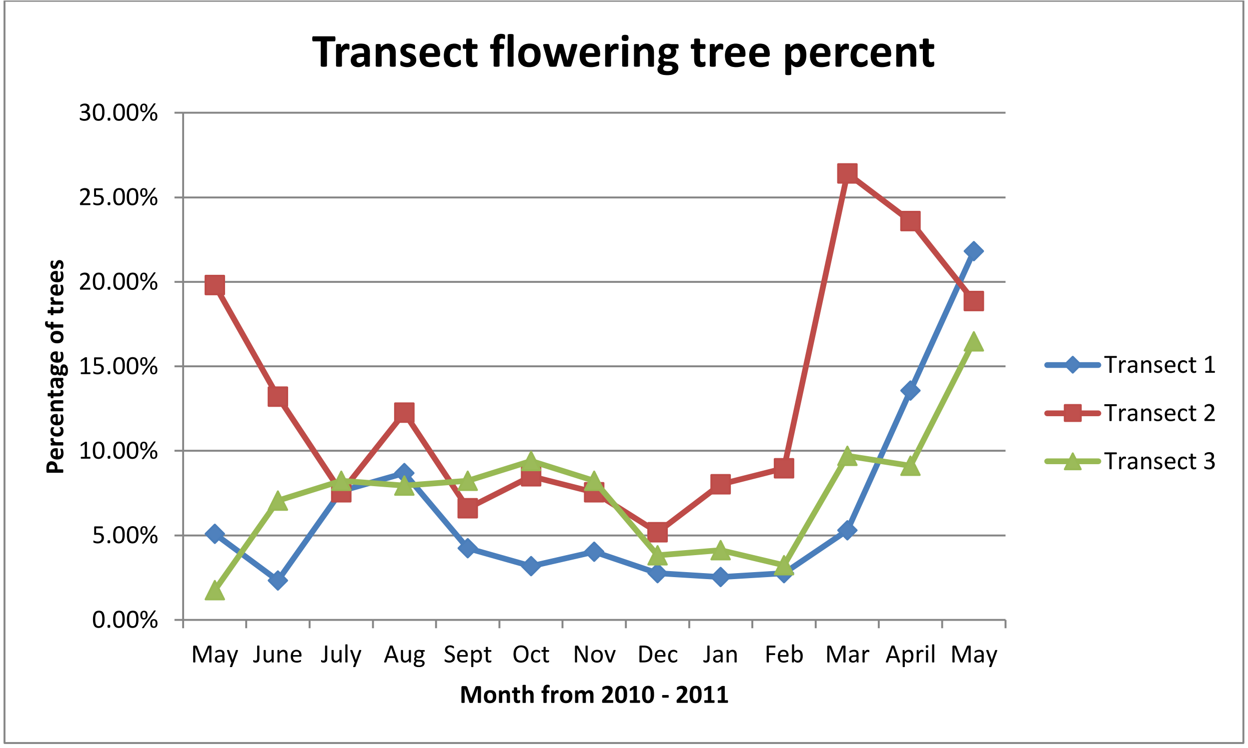
Figure 4.21. Fruiting and precipitation (dry season is February through May).



4.3.9. Masting

Masting events typically involve the mass flowering of dipterocarp and non-dipterocarp trees growing in dipterocarp forests (Ashton et al., 1988; Sakai, 2002). As illustrated in Figure 4.23, the percentage of flowering trees during the 2010 flowering season more than doubled in the 2011 flowering season on Transect 1 and Transect 3. In Transect 1 this increased from 5% in May 2010 to 22% in May 2011, and in Transect 3 this increased from 2% in May 2010 to 17% in May 2011. Both of these transects contain dipterocarp trees and are located in and/or near areas dominated by dipterocarp trees. Transect 2 however is not characterized by masting flowering synchrony, with about equal number of trees flowering in May of both flowering seasons, although it has a significant number of trees flowering each year.

Figure 4.22. Masting events in transect flowering.



4.3.10. Phenology of *Parashorea stellata*

Given the dietary importance of *P. stellata* to red-shanked doucs on Son Tra (Chapter 7), the structural and phenology patterns of *P. stellata* are here reported separately. On Transect 1 there were 42 individuals of *P. stellata*, two of which were dead when this transect was established. They comprised 17.8% of Transect 1 trees. Although this species is little studied, basic ecological information is known (Luu Hong Truong, personal communication, 2013; Rachun Pooma, personal communication, 2012). The reported distribution for this species is in Myanmar, Laos, South Vietnam and Malay Peninsula, it grows in evergreen dipterocarp forests up to 1000 m and typically on mountain slopes, tree height is between 20 to 50 m and buttressed at two to three m, DBH averages between 80 and 100 cm, and it flowers between April and July and fruits between August and October (Nguyen Ngoc Chinh et al., 1996; Pham Hoang Ho, 1991; Pooma, 2003; Pooma & Newman, 2001; Poopath et al., 2012; Smitinand et al., 1980; Smitinand et al., 1990).

The average height of the *P. stellata* trees of Transect 1 was 15.89 ± 5.26 m, DBH was 45.42 ± 27.74 cm, and crown width was 9.29 ± 5.28 m. These averages are all greater than the averages of any transect. However, these averages are also less than reported averages for this species. The five highest trees of all transects were *P. stellata,* on Transect 1 the 13 highest trees were *P. stellata* and the two highest of these were 26.1 m each. This species dominated the canopy of Transect 1 and occupied a SBA of 23.4 m^2/ha, which is nearly half of the total SBA of this transect.

Of the 40 living *P. stellata* trees on Transect 1, 95.58% produced young leaves each month and 9.62% had a leaf flush of 25% or greater each month. Figure 4.23 shows the percentage of *P. stellata* trees with total leaf flush, illustrating that most had young leaves available throughout the year, and 100% of the trees had young leaves available from October through May. Fewer trees had leaf flush in May and July to August. Figure 4.24 shows leaf flush at 25% or greater illustrating that leaf flush in *P. stellata* follows the pattern generally observed in this study. Leaf fall in *P. stellata* also follows the general pattern with leaf fall occurring during the dry season months (Figure 4.24). During the study period only a single *P. stellata* tree produced flowers in 2010 (June). However during 2011 towards the end of transect records 49% of the trees were producing flowers and the number may have continued to increase (Figure 4.24) indicating "general flowering", a rare masting event unique to dipterocarp forests as described above. Unfortunately due to a lack of personal understanding of the distinctiveness of this event, it was not completely recorded.

Figure 4.23. Percentage of *P. stellata* trees producing over 1% young leaves (dry season is February through May).

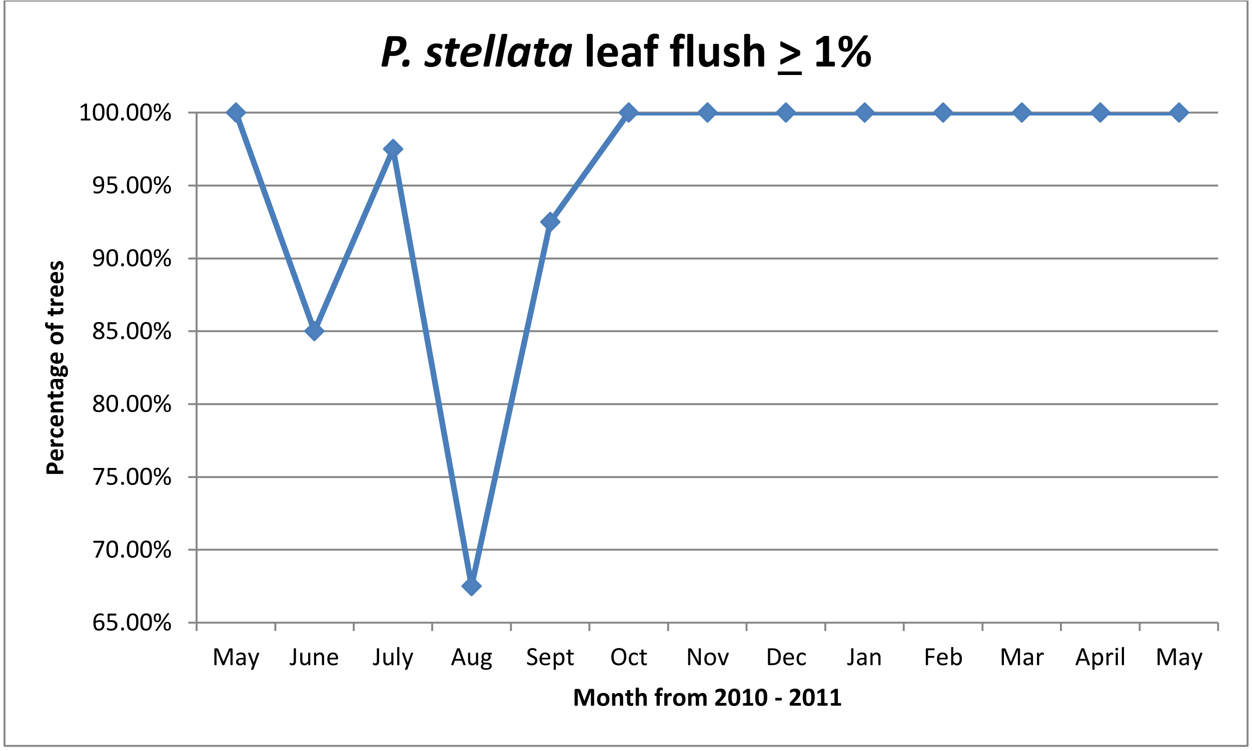
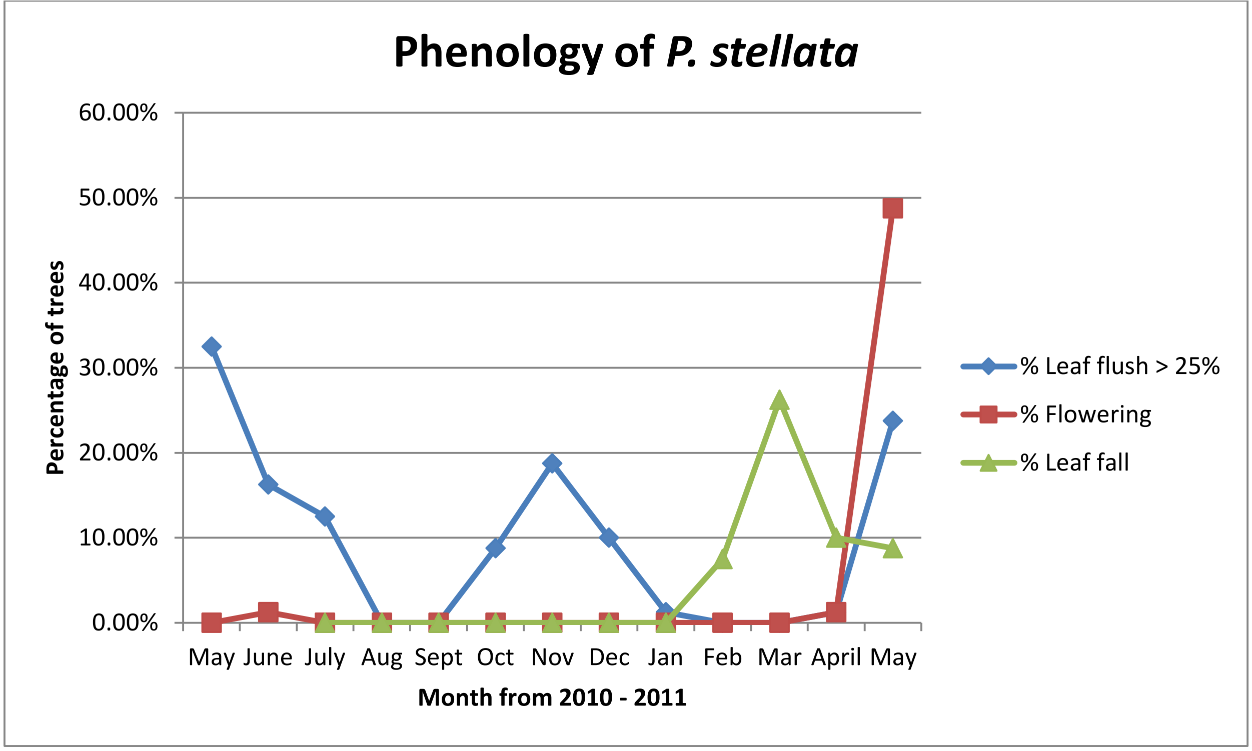


Figure 4.24. Phenology of *P. stellata*.
Showing percentage of trees producing above 25% young leaves, percentage of trees with any amount of leaf fall, and percentage of trees producing any amount of flowers.



4.4. Discussion

4.4.1. Transect composition

Discussions of family level richness and diversity permit for basic comparisons between transects. Euphorbiaceae is a dominant family in all transects, being the second most abundant family along Transect 1 and 3, and the dominant family of Transect 2. Dipterocarpaceae dominates Transect 1 in number, height, crown width, and SBA. Transect 3 has several families contributing more equally to the proportion of trees, and of these Sapindaceae is most dominant.

Combining all transect trees, the six most dominant families noted in this study were Euphorbiaceae (17.4%), Myrtaceae (11.3%), Dipterocarpaceae (9.6%), Sapindaceae (8.4%), Anacardiaceae (6.8%) and Lauraceae (6.6%). In Kon Ka Kinh National Park, Vietnam where grey-shanked doucs were studied (Ha Thang Long, 2009), the six most dominant families of combined transects were Euphorbiaceae (10.0%), Sapindaceae (9.4%), Lauraceae (8.9%), Myrtaceae (8.6%), Guttiferae (8.0%), and Fagaceae (7.0%). Kon Ka Kinh and Son Tra share four of their top six dominant tree families, with the most dominant family in both as Euphorbiaceae. Of all current *Pygathrix* studies, the forests in Kon Ka Kinh National Park are most comparable to Son Tra Nature Reserve. These two sites are both located in Central Vietnam.

In Seima Biodiversity Conservation Area, Cambodia where black-shanked doucs were studied (Rawson, 2009), the six most dominant families of combined transects were Fabaceae (17.5%), Lythraceae (14.9%), Lamiaceae (10.2%), Tiliaceae (10.2%), Combretaceae (6.7%), and Bignoniaceae (4.7%). There is a complete lack of overlap with the dominant families reported in this study, and a single overlap with those reported in Kon Ka Kinh.

4.4.2. Transect structure

Ha Thang Long (2009) reported the forests in Kon Ka Kinh were mixed evergreen and semi-evergreen. The timing and duration of the dry (December through April) and wet (May through November) seasons in Kon Ka Kinh were generally comparable to Son Tra. Mean heights of trees in Kon Ka Kinh (11.2 to 14.0 m) were comparable to Son Tra (8.7 to 9.8 m). In both studies there were few trees over 25 m. The average range of DBH values (24.2 to 28.0 cm) was similarly comparable to Son Tra (20.2 to 27.9 cm), and the distribution of DBH values was also comparable. SBA was comparable between Kon Ka Kinh (44.7 to 65.6 m^2/ha) and Son Tra (43.1 to 56.9 m^2/ha). Average tree density in Kon Ka Kinh (580 to 684 trees/ha) was generally comparable to Son Tra (442 to 708 trees/ha).

Rawson (2009) studied the black-shanked doucs in the semi-evergreen (mixed deciduous) forests of Seima Biodiversity Conservation Area, Cambodia. The timing and duration of the dry season (November through April) and wet season (May through October) were different than in Son Tra. Mean heights of trees on his three transects (14.1 to 17.7 m) were higher and contained a greater percentage of trees over 25 m than in Son Tra. DBH averages ranged from 23.1 to 26.4 cm, which is comparable to Son Tra (20.2 to 27.9 cm). SBA was lower than in Son Tra, ranging from 28.0 to 33.5 m^2/ha. Density was lower in Seima (350 to 507 trees/ha). Differences between forests examined by Rawson (2009) and those on Son Tra can be contributed first to different forest types, although disturbance and regeneration influence forest structure.

Millet et al. (2010) analyzed disturbed secondary forests in Vietnam over 25 plots, and reported the average density was 587 trees/ha and SBA was 26 m^2/ha. Density is comparable to Transect 1 and 2 in this study, but the low SBA suggests the plots they analyzed were significantly logged or mature forest that had been recently disturbed. In their study the percentage of trees with DBH below 20 cm was 63%, trees above 50 cm DBH was 3.8% and 1/3rd of the plots contained no trees with a DBH above 80 cm. The distribution of DBH values is similar to the values found on transects in this study.

The studies of Millet et al. (2010) and Blanc et al. (2000) support the classification of Son Tra forests as regenerating secondary forest, and the comparability with undisturbed wet tropical forests of Kon Ka Kinh indicate the secondary forests on Son Tra are of excellent quality. Tropical lowland forests such as those on Son Tra are among the most threatened worldwide and in Vietnam they are heavily disturbed (Millet et al., 2010). In Vietnam, Cambodia and Laos, doucs and other primates inhabit largely disturbed forests, and evaluating undisturbed floristic compositions has become increasingly difficult.

4.4.3. Transect tree mortality

Tree mortality was calculated by Lewis et al. (2004a; 2004b) over 31 years in South America. They reported an average tree mortality of 1.6% per year. Rawson (2009) reported similar results with a mortality rate of 1.55% of transect trees per year. These estimates are lower than the 2.9% tree mortality observed in this study. However, this estimate is probably inflated because it contains data from 13 months, I included four trees which were dead during transect establishment, and three trees were dying during the end of the study but they were not confirmed dead aside from an absence of leaves and leafing over a month. Removing these trees from the analysis results in a 1.56% mortality rate which is similar to the mortality rate noted in the above studies. Lewis et al. (2004a) showed that the mortality rates within a single plot could fluctuate between 1.5 and 3.5%, and in an extreme case even between 0.9 and 4.5%. If all dead (or dying) trees on Transect 1 are included, this indicates there is a high mortality of trees on this transect (5.1%), which is above the high values established by Lewis et al. (2004a).

There are several possible reasons for the high mortality of trees along Transect 1. As noted, this transect had the densest upper canopy and therefore less light reached the lower canopies and forest floor, and it had a relatively high tree density and SBA and therefore a high degree of competition between trees. This may account for some of the recorded deaths. Because transect trees were not identified to species level or aged, comparing mortality to species and age is not possible. It is unlikely that these deaths are related to changes in weather, such as extremes in temperature, because the weather patterns during the study period closely followed data over the last 20 to 50 years (see Chapter 3). Physical synchronous major episodic mortality events such as catastrophic windfall or extreme precipitation caused by tropical storms (Carey et al., 1994) remain a possibility and indeed precipitation during the study period was above the average during the wet season (see Chapter 3). It seems more likely that tree mortality on Son Tra was related to chemical or biological factors. Predictions for increases in tree mortality (see Carey et al., 1994; Lewis et al., 2004b) include a) increases in acidity of rainfall which could be related to industrial activities in and around Da Nang City, b) liana and vine loading leading to increased tree mortality, c) increases in edge effects due to increasing encroachment, d) fragmentation and the pioneer effect as increased fragmentation leads to pioneer species invading remaining forests, and e) floral disease or insect infestation. A combination of multiple factors likely influences tree mortality on Son Tra. Concerning pioneer effects, Son Tra forests are greatly threatened by the invasive climber *Ipomoea eberhardtii* (white bells) which grows over, smothers and eventually kills trees. This climbing vine is a severe threat to remaining forests on Son Tra (China Daily, 2004; Dinh Thi Phuong Anh et al., 2010). However, this species was not observed along or near any transect. Concerning floral disease or insect infestation, there was no apparent evidence of Son Tra tree mortality being related to these biological factors. Finally, it also seems unlikely that acidic rainfall, excessive rainfall, or edge effects are causes for the observed tree mortality on Son Tra because the mortality was primarily localized to Transect 1. Localized conditions may provide a greater explanation, including tree competition and the amount of sunlight reaching lower levels of the canopy. Liana competition, as noted by Lewis et al. (2004b) and Perez-Calicrup & Barker (2000), may also contribute to increased tree mortality along Transect 1 which had a larger number of lianas and vines compared to the other transects. However, competition was greatest among Transect 3 where only one tree died during the study.

Data gathered in this study does not permit me to deduce the reasons for the observed tree mortality on Son Tra

4.4.4. Phenophase patterns

4.4.4.1. Leaf flush

Leaf flush occurred at the end of the dry season and start of the wet season. In a tropical seasonal environment it is typical for trees to produce new leaves during this time (Daubenmire, 1972; Frankie et al., 1974; Lieberman, 1982; van Schaik et al., 1993). As Janzen (1967) noted, this is likely because rapid vegetative growth is essential at this time if a tree (or species) is to remain competitive with its neighbors. All energy is therefore channeled into new growth, usually at the expense of flowering. In this study, leaf flush is timed to the increase of water availability. During May, which is classified as a dry season month, precipitation averages 40 mm, and in July during the wet season this increases to 129 mm. Janzen (1967) indicated that early rains result in leaf flush, and Borchert (1994) indicated that dry season leaf flush is possible when rains exceed 30 mm in a month. It is possible that late dry season leaf flush on Son Tra is related to precipitation as an external stimulus and not photoreceptive period, as is suggested for drier forests (Elliot et al., 2006; Rivera et al., 2002). Ha Thang Long (2009) and Rawson (2009) both reported leaf flushing during the dry season just before the onset of the wet season. This study noted that most trees have some leaf flush throughout the year. Frankie et al. (1974) recorded nearly half of the trees in tropical environments continually produced new leaves. Janzen (1967) also noted most tropical trees have leaves at various stages of development throughout the year, and therefore minimal amounts of leaf flush throughout the year is common. Ha Thang Long (2009) and Rawson (2009) both noted leaf flush availability throughout the year.

4.4.4.2. Leaf fall

Leaf fall was concentrated during the dry season, which is similar to semi-evergreen dry and wet tropical forests (Daubenmire, 1972; Frankie et al., 1974; Ha Thang Long, 2009;

Lieberman, 1982; Rawson, 2009; Reich & Borchert, 1984; van Schaik et al., 1993). During the dry season months on Son Tra between 72% and 86% of the trees on transects lacked leaf fall, strongly suggesting evergreen status of forests on Son Tra. In temperate environments leaves are shed as day length shortens, and photoperiod is the determining external stimulus. Day length was not analyzed in this study, but there was a significant correlation between leaf fall and seasonality (*i.e.*, leaf fall occurred only during the dry season and never reached 1% of the trees during any month of the wet season). Reduction in precipitation during the dry season therefore appears to be a strong external stimulus for leaf abscission on Son Tra.

4.4.4.3. Flowering

This study recorded a monthly range between 3.9 and 15.7% transect trees flowering, comparable to Rawson (2009) who recorded between 1 and 16%, and to Ha Thang Long (2009) who reported between 2.5 and 19%. In tropical seasonal environments flowering typically peaks during the dry season, and usually follows peaks in leaf fall or immediately precedes (or coincides with) peaks in leaf flush (Borchert, 1983; Daubenmire, 1972; Frankie et al., 1974; van Schaik et al., 1993). These patterns were observed in this study. The reason for this may relate to visibility of flowers and ease of access to flowers during high insect pollinating activity (Janzen, 1967), which accounts for 96% of pollination in tropical semi-evergreen forests, as reported by Daubenmire (1972).

As has been observed in other studies of tropical forests (Frankie et al., 1974; Ha Thang Long, 2009; Rawson, 2009) there were two flowering peaks on Son Tra, including a primary peak during the dry season and shorter secondary peak during the wet season.

4.4.4.4. Fruiting

This study observed a peak in fruiting towards the end of the wet season in November, and a slightly smaller peak during the end of the dry season and beginning of the wet season between May and August following the primary flowering peak. Fruiting peaks are commonly reported during the end of the dry season and beginning of the wet season in tropical forests (Frankie et al., 1974; van Schaik et al., 1993). The timing of the wet season fruiting peak was slightly different in all transects. When all transect trees are combined, monthly averages of trees producing fruit ranged from 1.8% to 6.2%, indicating fruit is available throughout the year as has been described for tropical forests (Daubenmire, 1972). Fruiting peaks were not as pronounced as peaks in leaf flush or flowering, which is also described for tropical forests (Daubenmire, 1972). The percentage of transect trees fruiting in this study were notably less than the monthly ranges reported by Rawson (2009) (~5 to 21%) and Ha Thang Long (2009) (~1 to 22%). Fruit availability on Son Tra is therefore low in comparison. Fruiting during the end of the dry season and early wet season contained fruits which possessed wind-adapted disseminules, but wet season fruits did not contain these structures. Wind-adapted fruiting during the dry season has been described as beneficial to dispersal as opposed to wind dispersal during other times of the year (Daubenmire, 1972; van Schaik et al., 1993). Fruiting during this time decreases seedling mortality (van Schaik et al., 1993). Primarily dry season fruiting was reported by Rawson (2009) which is typical for dry tropical forests, and primarily wet season fruiting was reported by Ha Thang Long (2009) which is typical for wet tropical forests. Fruiting phenology on Son Tra was bimodal, with the percentage of trees fruiting during wet and dry season peaks being similar, suggesting Son Tra forests are a mix between dry and wet tropical forest types.

4.4.5. Dipterocarp forests

Although Son Tra contains only a few dipterocarp species, the influence these trees have on the forest is important.

Parashorea stellata was one of the transect trees identified to species level, and was dominant on Transect 1. Dipterocarp trees dominate the emergent canopy of forests wherever they grow. They are mostly confined to wet tropical climates in which the dry season is four months or less because most are evergreen (Ashton, 1988), but can occur in drier forest types. Their occurrence indicates that a forest is in its mature phase as these trees can only grow after a closed canopy is established (Ashton, 1988; Ashton et al., 1988; Sakai, 2002). Son Tra has dipterocarp trees that dominate the canopy of several slopes, but its abundance appears to be less than when reported by Van Peenen et al. in 1971.

During this study a single dipterocarp tree was observed to flower during 2010, but general flowering was observed in 2011, and after transect recording was completed mass fruiting was observed during June and July 2011. General flowering and the proceeding mass fruiting events are a phenomenon in tropical biology (see Ashton, 1988; Ashton et al., 1988; Sakai, 2002). These masting events occur at irregular intervals over multiple years, generally between two to 10 years apart (Ashton et al., 1988; Sakai, 2002) and involve the masting of both dipterocarp trees and the trees of other families (Ashton et al., 1988). As is typical of these events, all areas of Son Tra forests which contained *P. stellata* trees were flowering and fruiting in synchrony, which is to be expected to assure cross-pollination. However, it is unclear which external or internal stimuli lead to masting. Some researchers have suggested severe drought (Brearley et al., 2007; Janzen, 1974; van Schaik, 1986), excess rain (Appanah, 1985), photoperiod (Ng, 1977), decreases in the minimum average temperature (Ashton et al., 1988;

Yasuda et al., 1999), decrease in average nighttime temperatures (Appanah, 1993), and reduction in seed-predation rates (Janzen, 1971; Kelly, 1994; Sork et al., 1993). Masting has been correlated with increases in vertebrate reproduction and ranging, and can have significant effects on tree population numbers, structure, and growth over a short time (Curran & Leighton, 2000). Given the relative normalcy of weather during the research period, weather might not be the determining external stimulus for the observed masting. There was notably more precipitation during the study period than previous years, but data gathered during this study does not permit for an analysis of stimuli related to masting.

Dipterocarp trees face the risk of local extinction on Son Tra (Lippold & Vu Ngoc Thanh, 2008). In particular, *P. stellata* is continuously harvested for resin. There is also small scale logging, and dipterocarp trees are a target tree as they generally dominate the international hardwood markets and are used for construction of homes, boats and furniture in Vietnam (Ashton, 1988; Nguyen Ngoc Chinh et al., 1996). Furthermore, the impacts of climate change on dipterocarp forests cannot be ignored (Corlett & La Frankie, 1998). As noted by Van Peenen et al. (1971) and in this study, the elevations above 300 m on Son Tra are often shrouded in clouds during all months, permitting for moist environments to which dipterocarp trees are adapted. All dipterocarp trees on transects in this study were found above 300 m, which is partly why Transect 2 lacked these trees (see Table 4.2). Climate change resulting in increasing drought and reduction of cloud cover on Son Tra, coupled with the modification of forests (harvesting of trees, lianas and resins, increasing carbon dioxide levels, increasing fragmentation and edge effects) could result in greater losses of the important *P. stellata* and other dipterocarp trees.

4.5. Conclusion

The phenology of Son Tra is greatly influenced by the dry season decrease in precipitation. Son Tra is considered a dry tropical semi-evergreen forest because of the average annual precipitation. Due to the moisture above 300 m it likely also approaches a wet tropical semi-evergreen forest, a classification which is supported by the presence of areas dominated by dipterocarp trees and wet season increases in fruiting. Son Tra forests resembles both dry and wet tropical forests in that there is deciduousness during the dry season, increases in leaf flush and flowering at the end of the dry season and beginning of the wet season followed closely by a peak in fruiting, and has a peak in flowering and fruiting in the mid to late wet season. Transects suggest the forests of Son Tra are heterogeneous and disturbed, although many areas are characterized by excellent secondary forest. All transects are comparable in structure, including Transect 3 which was in a previously disturbed forested area (see Van Peenen et al., 1971). Transects had different species compositions and the top three dominant families were generally different between transects. A particularly significant event in the phenology cycle was the masting of dipterocarp trees which are important to the doucs on Son Tra.

Chapter 5. Group composition, organization, size, ranging, and other social behaviors

5.1. Introduction

5.1.1. Chapter preview and terminology

Our understanding of the social organization and structures among populations of *Pygathrix* are evolving (Ha Thang Long, 2009; Hoang Minh Duc, 2007; Phiapalath, 2009; Phiapalath et al, 2011; Rawson, 2009). The introduction reviews our current understanding and the factors influencing social organization and ranging. Statistical methods are presented. Results are divided into four sections. The first section analyzes unit and group composition, organization and size, and the second section reports on fission-fusion and unit cohesion. The third section analyzes ranging patterns including home range, core area, home range overlap, and daily path lengths. The final section describes observations of super-trooping, bachelor individuals, all-male units, immigration and emigration, birthing, and interspecific associations.

The term "group" if applied to *Pygathrix* refers to the social organization comprised of multiple units. The term "unit" refers to family units or reproductive units, similar to some colobines studies (Mulder, 2012; Rawson, 2009), or the definition of "group" (Fuentes, 2011). The term unit as used here is referred to as subgroups, subunits, foraging units, bands, parties or groups in various studies, occasionally with multiple terms used to describe the same social organization (for example see Chapman et al., 1995; Chapman & Rothman, 2009; Fuentes, 2011; Grueter & van Schaik, 2010; Hoang Minh Duc, 2007; Kirkpatrick, 2011; Peres, 1996; Sicotte, 1993; Strier, 1991; Symington, 1988; Xiao Guang Qi et al., 2009). The distinction between units and groups is rarely made in *Pygathrix* research partly due to a lack of habituation, with the exception of Hoang Minh Duc (2007) who is the first researcher to make a clear distinction between units and groups. In certain reports it is clear if the researcher is referring to a unit or group even if the distinction was not made. In other reports this distinction remains unclear, and I use the term “unit/group” when referencing their data. I use the term “super-troop” to refer to the fusion of multiple groups. When referencing a study reporting group sizes that likely reflect a super-troop I use the term “group/super-troop”. The term “super-troop” or “super-group” has been used to describe this social organization in primates (Caldecott et al., 1996; Cords, 2012; Gartlan, 1970; Gautier-Hion et al., 1999; Grüter, 2003).

The term “home range” refers to the area of land which the doucs regularly use (Fleagle, 2013; Jolly, 1972; Wilson, 2000). My use of this term is comparable to “total range” (Wilson, 2000). Variation in ranging between seasons and months is the variation in the use of home range (Curtis & Zaramody, 1998; Robbins & McNeilage, 2003), also referred to as variation in core area (Harris & Chapman, 2007). “Core area” is the area of heaviest use in a home range (Feldhamer et al., 2007; Harris, 2006; Wilson, 2000).

5.1.2. Review

Knowledge of group size, unit size, group composition and ranging among *Pygathrix* has increased significantly in recent years. Lippold (1977) reported group structure among red-shanked doucs as one-male and multi-male units with an average unit/group size of nine individuals. She observed bachelor individuals of both sexes and fission of groups into units. Pham Nhat (1993b) and Ratajszczak et al. (1990) estimated unit/group size of *Pygathrix* between four and 30 individuals. Lippold (1998) reported group/super-troop size of red-shanked doucs as high as 51 individuals, a black-shanked douc group/super-troop of 36 individuals at the same site, and suggested group size was related to habitat variation and anthropogenic effects. Hoang Minh Duc (2007) reported black-shanked douc group sizes of 13 to 23 individuals, unit size to be eight to nine individuals, and noted encounters of groups/super-troops up to 45 individuals. He did not observe group sizes to differ between habitat types, and rarely observed bachelor individuals. Rawson (2009) reported unit size of black-shanked doucs at seven individuals ranging from one to 26 individuals, with the higher end of this range clearly reflecting groups. He observed bachelor individuals, and fission of groups into units. Unit/group size increased in the wet season, but sizes did not differ between habitat types. Ha Thanh Long (2009) reported group size of grey-shanked doucs was 14.8 individuals, ranging from two to 88 individuals. He observed one-male units, multi-male units, all-male units and bachelor individuals. Units/groups and groups/super-troops fused for up to three days, fused more frequently when young leaves were abundant and fissioned more frequently when fruits were abundant (Ha Thang Long, 2009). Phiapalath (2009) reported red-shanked douc group size at 15 individuals ranging from three to 40 individuals. Phiapalath et al. (2011) reported unit/group size decreased during the dry season when high quality foods were scarce.

Sex ratio of *Pygathrix* averages 1:2 adult males to females, ranging from 1:1.8 to 1:2.7 males to females (Hoang Minh Duc, 2007; Lippold, 1977; Lippold, 1998; Ha Thanh Long, 2009; Pham Nhat, 1993b; Phiapalath et al., 2011; Rawson, 2009).

Phiapalath (2009) reported the home range of *P. nemaeus* at 292 ha, although it is unclear if the area represents the home range of a single group or multiple groups. He also reported ranging variability between the dry season during high quality food scarcity (253 ha), and the wet season during high quality food abundance (113 ha). Hoang Minh Duc (2007) reported the home range of *P. nigripes* groups was between 42 and 47 ha with a 976 m daily path length (658-1666 m). In contrast to Phiapalath, he found range use increased during the wet season when high quality foods were abundant, and decreased during the dry season when high quality foods were scarce (Hoang Minh Duc, 2007). Daily path lengths however did not differ between wet and dry seasons, but they were shorter on days with higher precipitation. Rawson (2009) reported home range for units/groups of *P. nigripes* at 20 ha and a daily path length of 943 m. Ha Thanh Long (2009) calculated home range for a group/super-troop of grey-shanked doucs at 984 ha, and a daily path length of 1068 m ranging between 50 to 4080 m.

5.1.3. Influencing factors

Unit and group sizes, their structures and ranging behavior depend on many variables including weather and the influence of weather on plant phenology, food availability and distribution (Bleisch & Jiahua Xie, 1998; Clutton-Brock, 1975; Dias & Strier, 2003; Fedigan & Jack, 2001; Isbell, 1983; Jolly et al., 2002; Matsuda, 2008; Moura, 2007; Newton, 1992; Oates, 1987), habitat type and structures (Eisenberg et al., 1972; Emmons, 1984; Harris & Chapman, 2007; Jolly et al., 2002; Nowak & Lee, 2011; Roese et al., 1991), mixture of habitat patches and an animal's experience with those patches (Folse et al., 1989), mate location and the allee principle (Wells et al., 1998), mating cycles (Kirkpatrick, 1998), mating systems and female monopolization (Clutton-Brock & Harvey, 1977; Korstjens & Noe, 2004; Newton, 1988; Tong Jin et al., 2009; Wrangham, 1980), infanticide risk (Borries et al., 1999; Teichroeb et al., 2012), predation by other animals (Busse, 1977; Cheney & Wrangham, 1987), foraging strategies (Moura, 2007), digestibility of fall-back foods (Korstjens & Dunbar, 2007), food quality (Fashing et al., 2007a), interspecific competition (Angedakin & Lwanga, 2011; Kamilar & Ledogar, 2011; Senf, 2009), intraspecific competition and range overlaps (Borries et al., 2008; Dunbar, 1987; Gillespie & Chapman, 2001; Struhsaker & Leland, 1988), phylogenetic inertia (Chapman & Rothman, 2009), digestive physiology (Korstjens & Dunbar, 2008), time allocated to resting (Pollard & Blumstein, 2008), habitat fragmentation (Chiarello & Melo, 2001; Decker, 1994; Martins, 2005), habitat disturbance (Anderson et al., 2007; Fashing, 2011), and other anthropogenic effects (Ha Thanh Long, 2007; Pinto et al., 1993; Pinto et al., 2009).

The above socioecological forces are not mutually exclusive. For example, group sizes of *Pygathrix* have been reported to depend on the degree of hunting and habitat pressures (Ha Thang Long, 2007; Lippold, 1998). Boonrattana (2000) reported food availability and the proportions of foods in diet affect ranging. Steel (2012) suggested food species diversity and food species selectivity influence ranging. Fleury & Gautier-Hion (1999) reported changes in staple food quality accounts for variations in ranging but not for variation in group size. Clutton-Brock & Harvey (1977), Dias & Strier (2003), Dunbar (1987) and Isbell (1991) reported group size affects home and day range because larger groups require larger ranges. Isbell (1991) also noted that ranges are related to food abundance and food patch distributions.

Some of these studies are based on the ecological-constraints model which suggests that larger group sizes or interspecific associations have the benefit of decreasing predation risk, but do so at the cost of increasing intragroup competition, and necessitate increased home and/or day ranging to meet nutritional requirements (Gillespie & Chapman, 2001; Steenbeek & van Schaik, 2001). Gillespie & Chapman (2001) and Teichroeb & Sicotte (2009) reported the ecological-constraints model is applicable to folivorous colobine primates, although Yeager & Kirkpatrick (1998) did not support this relationship among Asian colobines. Snaith & Chapman (2007) indicated group size, organization and structure are influenced by several factors, and therefore variability in the applicability of the model is expected.

Southwick et al. (1980) illustrated that group sizes, structure and organization are indications of population maintenance requirements and thus an indication of population viability. Understanding of these characteristics is essential to evaluate the minimum unit or group size for population viability analyses (Young & Isbell, 1994). These data are important given the endangered status of *Pygathrix* and because these primates live in small fragmented populations in Vietnam. According to Young & Isbell (1994) population extinction is likely if groups (or units) fall below a minimum size, even if at a larger scale of analysis the population is above a critical size. Similarly, Wells et al. (1998) noted that low population densities result in reduction of mate location efficiency and can lead to extinction. Young & Isbell (1994) further noted that fusion minimizes the negative effects associated with minimum group size. Knowledge of group size, structure and organization is critical to understanding population viability among *Pygathrix*.

5.2. Methods of data analysis

Unit sizes are analyzed, compared between seasons using the Mann-Whitney U test with two tails at p=0.05, and compared to weather and phenology data using Pearson's Correlation coefficient with two tails at p=0.05. Pearson's Correlation coefficient is regularly used because it analyzes linear relationships, and because significance is more stringently tested. Only encounters which allowed a full count of the unit are included, and repeat counts of the same unit are removed. Group size is only reported for the three main research groups which were repeatedly observed. These groups were located in different areas of Son Tra. All encounters with doucs other than the three research groups were considered to be unit encounters given their composition and small size. Unit composition is reported descriptively, involving only encounters from which the exact unit composition could be recorded. Additionally, the observed unit had to contain at least one adult female and one adult male to be included in the composition analysis.

Range analyses are conducted for the primary research group. Analyses were conducted with MapInfo Professional 10.0. Home range was calculated using the minimum convex polygon method. Based on my observations, the primary research group used all areas within their home range; therefore the entire area within the polygon represents their home range. Ranging variation in the use of home range is analyzed seasonal and monthly using the minimum convex polygon method. Core area is analyzed by kernel density modeling and is defined as 50% kernels. Seasonal and monthly variation in ranging are compared to weather and phenology data using Pearson's Correlation coefficient with two tails at p=0.05. An estimated degree of home range overlap was based on sightings of different groups and corresponding GPS marks inside the home range of the primary research group. Adjacent groups were only observed near each other along the borders of their home range, and therefore a convex polygon would bisect the home range resulting in an overestimated degree of overlap. Therefore the minimum convex polygon method is not appropriate and concave polygons are used for a basic analysis. Daily path length is analyzed and compared to weather and phenology data using Pearson's Correlation coefficient with two tails at p=0.05. Daily path lengths are the sum of straight lines connecting GPS marks. Only full-day follows are used for daily path length analyses (see Chapter 3).

Fission and fusion between units is first analyzed with data derived from unit size averages, and analyzed second based on direct observations of fission and fusion events. A fission-fusion event involved observing either the fission or fusion itself or the observation that units were fused or fissioned when encountered. Events were recorded with certainty; if it was unclear how many units were together, if the units were together, or if the units had separated no fission-fusion event was recorded. During a full-day follow multiple fission-fusion events could be recorded. Units were considered fused if they were within about 30 m of each other, and fissioned beyond this boundary. This distance was selected because it often translated to a physical separation of one or two trees between individuals; a separation that was often observed when units/groups would travel. Whenever units fused or a group fissioned the time was noted and the duration of time for which the fused or fissioned state occurred was recorded until the unit or group was lost or asleep in the evening. Fission and fusion events are compared to weather and phenology data using Pearson's Correlation coefficient with two tails at p=0.05. They are analyzed on a daily and seasonal scale, and compared between seasons using the Mann-Whitney U test with two tails at p=0.05.

Super-trooping is reported descriptively and compared to home range data. Observations of bachelor males, all-male groups, immigration, emigration, and birthing are reported descriptively and in relation to the three main research groups. Finally, interspecific associations between red-shanked doucs and rhesus macaques (*Macaca mulatta*) and between doucs and common muntjacs (*Muntiacus muntjak*) are described and compared to weather and phenology data using Pearson's Correlation coefficient with two tails at p=0.05.

5.3. Results

5.3.1. Unit and group composition, organization, and size

5.3.1.1. Composition and organization

The exact unit composition was recorded in 17 encounters after removal of repeat counts. The adult male to female sex ratio was 1:1.63 individuals. The ratio of adults to subadults to juveniles to infants was 3.7:0.8:0.8:1.5 individuals. The ratio of adults to immature individuals was 1.26:1 individuals. The average unit size based on these encounters was 6.8 ± 2.6 individuals. This is similar to the average unit size of the three main research groups calculated below, suggesting the sample is representative. Seven of the encounters contained more than one adult male (41.1%), indicating multi-male units are common. Of the 110 encounters from which partial to full group composition was gathered (*i.e.*, not all members were sexed or aged), which contained at least one adult male and one adult female, and excluding multiple counts of the same unit or group, 46 were multi-male (41.8%) and 64 (58.1%) were at least one-male units. Multi-male units were observed in all months of the study. All-male groups were only observed twice, they were not included in the evaluation of unit and group sizes or compositions, and are discussed later.

Data gathered on the group composition of the primary and secondary research groups was evaluated. The primary research group contained three units with a total number of 21 individuals at the end of research. The largest unit contained 12 individuals including two adult males, three adult females, one subadult female, one subadult male, one juvenile and four infants. Initially the subadult male was noted as juvenile but was subadult at the end of research. The next unit contained six individuals including one adult male, two adult females, one subadult female, one infant, and one recently immigrated subadult into the unit. The sex of this individual was not assessed with absolute certainty because it was rarely seen, but it was believed to be a female based on my observations and photographs. This individual immigrated into the unit in late March 2011 and did not come from any of the other units of this group. By conclusion of research activities in May 2011 this individual was still uncomfortable with researcher presence and remained out of sight except for brief observations. During the duration of research activities, the Forest Protection Department of Da Nang released a few trade confiscated doucs into Son Tra. Based on the behavior and sudden appearance of this animal, I assume this douc could have been a released individual. The smallest unit of the group contained three individuals including an adult male, adult female, and their juvenile offspring which matured since its initial record as an infant. No other changes in these units were observed, and the group remained stable from their first reliable unit composition observations in August 2010 through last observations in May 2011.

The secondary research group contained two units of 14 individuals. This group could be observed at a distance from 100 to about 1000 m across a valley and observations required the group to be on top of the canopy. The largest unit contained nine individuals including two adult males, three adult females, one subadult male, one juvenile, and two infants. The single change noted in this group involved the subadult male of this large unit, which towards the end of research was no longer observed traveling with his unit or the group. The smaller unit contained five individuals including one adult male, two adult females, one subadult female and one infant. There were no changes observed to this unit. Aside from the possible emigration of the subadult male, this group was stable from first reliable unit composition observation in March 2010 through last observations in May 2011.

An isolated unit from the tertiary research group was trapped in a small section of forest measuring about two ha created by road construction activities. This forest patch was bordered by the sea to the north, the road to the south, and was isolated from small strips of forest to the east and west by large landslides which were created during road construction. The unit was first observed in this location in May 2010 when road construction activities in the area began, and the doucs remained in this small forest patch until December 2010 when the road officially opened to the public. On the other side of the road were two additional units, which were continually observed near the road despite their access to the central forested block of Son Tra. Given their behavior, I assume these three units comprised a group that was separated by the road construction. The trapped unit contained one adult male, two adult females, one subadult female, one juvenile, one infant and one additional adult male which always remained separate from the unit by 50 to 100 m. One of the other units on the opposite side of the road comprised seven individuals including two adult males, two adult females, two adults or subadult which were unidentified, and one infant. The other unit contained a minimum of five individuals, with at least one adult male, two adult females, one infant and one unidentified individual.

These three groups are discussed throughout this dissertation. Of interest to group composition analysis is that all three groups contain both one-male and multi-male units. Group composition ratios of the three units of the primary group, two units of the secondary group, and the isolated unit of the tertiary group are compared to the other 11 encounters with known group composition. The six units from the research groups and the units of the other 11 encounters had the same sex ratio of 1:1.63 adult males to females. The adult to immature ratio in units of the research groups was slightly smaller (1.1:1.0 individuals) than the other encountered units (1.35:1.0 individuals). Despite this minor difference the units of the research groups are comparable to other units encountered. Because unit composition is similar I believe composition of the research groups is representative of groups on Son Tra Nature Reserve. This research supports the occurrence of multi-male/multi-female units and groups among red-shanked doucs.

5.3.1.2. Unit and group sizes

The exact unit size could be determined in 83 encounters after removal of repeat counts, encounter of super-trooping (n=3) and bachelor individuals (n=13). As noted previously, all encounters were with units, and group size can only be reported for the three main research groups.

The average size of units on Son Tra was 6.5 ± 1.2 individuals. If super-trooping and bachelor individual encounters are included the average size increases to 8.5 ± 5.0 individuals.

Group size analysis is based only on the three main research groups described above. The primary research group contained 21 individuals in three units, which is 3.5 times as large as the average unit size. The secondary research group contained 14 individuals in two units and the tertiary research group contained 19 individuals in three units. These groups are 2.1 and 2.9 times larger than the average unit size. Group sizes ranged from 14 to 21 individuals with an average of 18 ± 3.6 individuals and groups are composed of an average of 2.7 ± 0.6 units. Aside from a single birth, one immigration event and one possible emigration event, the individual unit size and structure did not change among the research groups. This is also alarming, considering this represents 54 individuals but only one birth during the research period.

Unit size was analyzed for comparisons between the wet and dry seasons with bachelor individual, super-trooping and repeat encounters removed (the research units are included in both seasons). In the dry season there where 42 encounters and unit size averaged 6.0 ± 2.9 individuals and in the wet season there were 51 encounters and unit size averaged 6.9 ± 1.3 individuals. Using Mann-Whitney U, there is no significant difference in the unit size between seasons. Considering unit sizes do not actually fluctuate seasonally, the observed fluctuation is a result of the degree of fission-fusion between units of groups.

5.3.2. Fission and fusion

5.3.2.1. Based on unit size

Monthly data on average unit size (like those reported above for seasons) broadly estimate the degree of fission and fusion (which is referred to as unit cohesion). Other than in the analyses of unit and group size, the super-trooping and bachelor individual encounters are included because these represent important aspects of fission and fusion patterns and cohesion, and provides for more robust monthly data.

There are numerous factors influencing the number of encounters with doucs per month such as the time spent in the field, precipitation, temperature, location of doucs and the researcher, habitat, density of the canopy, habituation, presence of other people in the forest, and the number of encounters with useful unit or group size observations. Monthly data therefore does not have a robust sample size, and includes a single count of the each of the units from the primary and secondary research groups (not the tertiary) to each month. Units of the tertiary research group were not included in every month because this group was not regularly observed throughout the study. Some months lacked encounters with any group aside from the primary and secondary research groups.

Figure 5.1 illustrates the average unit size per month. Unit size is fairly consistent between October and May. Between June and September the average unit size increases, which is partly the result of super-trooping events. However, unit size in August is also high and no super-trooping was observed in this month. This suggests the degree of fusion (units to groups and groups to super-troops) increases during the start of the wet season.

The criteria used to show monthly average unit sizes in Figure 5.1 is also used for analysis of unit size in correlation to leaf flush (Figure 5.2), flowering (Figure 5.3), fruiting (Figure 5.4), and with weather patterns (Figures 5.5 and 5.6). Phenology data collection began in May 2010, therefore the first three months of group size data cannot be compared to phenology patterns and are removed. The time frame of 13 months is also used for the analysis with weather data to provide for greater degree of comparison between variables.

Results indicate that unit cohesion is weakly correlated to temperature, precipitation, leaf flush, flowering, and fruiting. Among all correlations performed, temperature and unit size have the strongest positive relationship (r (13) = 0.54, p = 0.06), suggesting tendencies for increased fusion during warmer temperatures. Although my data does not support a significant correlation between unit size (and thus fission-fusion behavior) and external stimuli, if one exists it is not likely a single variable to variable correlation.

Figure 5.1. Monthly average unit size (dry season is February through May).

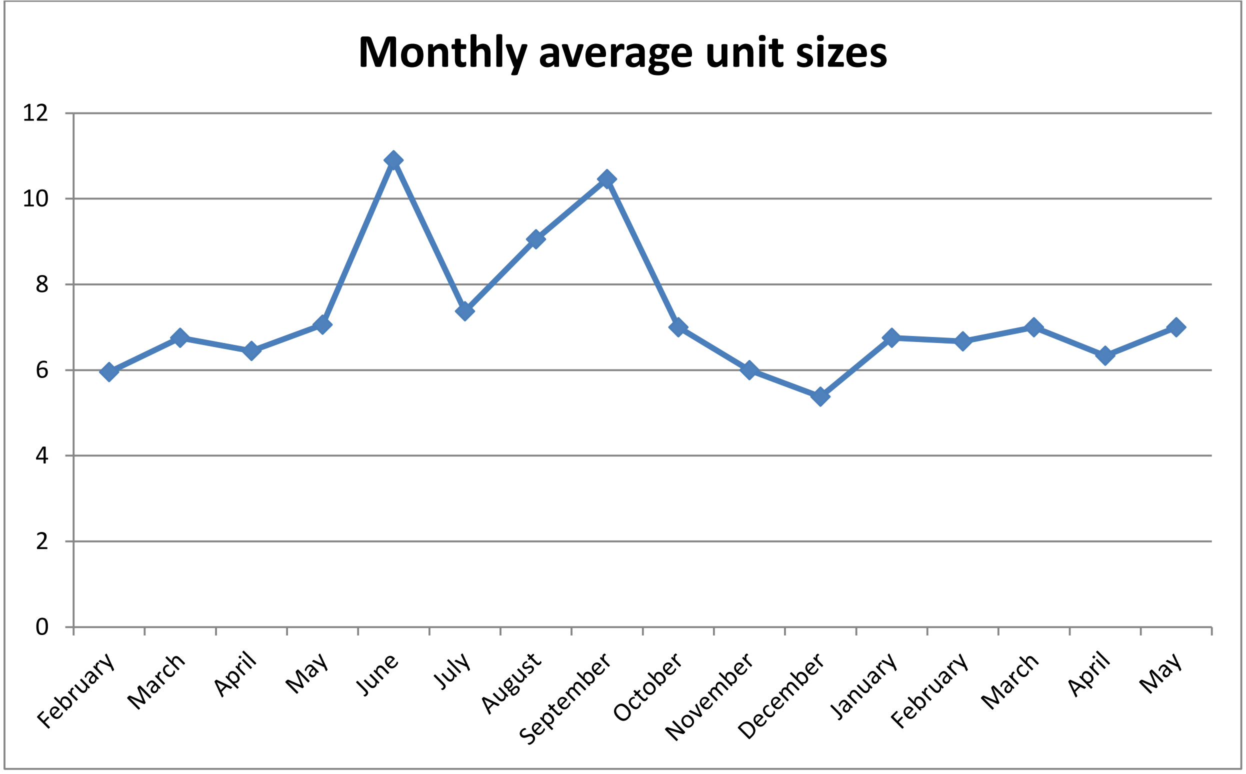


Figure 5.2. Leaf flush and unit size (dry season is February through May).

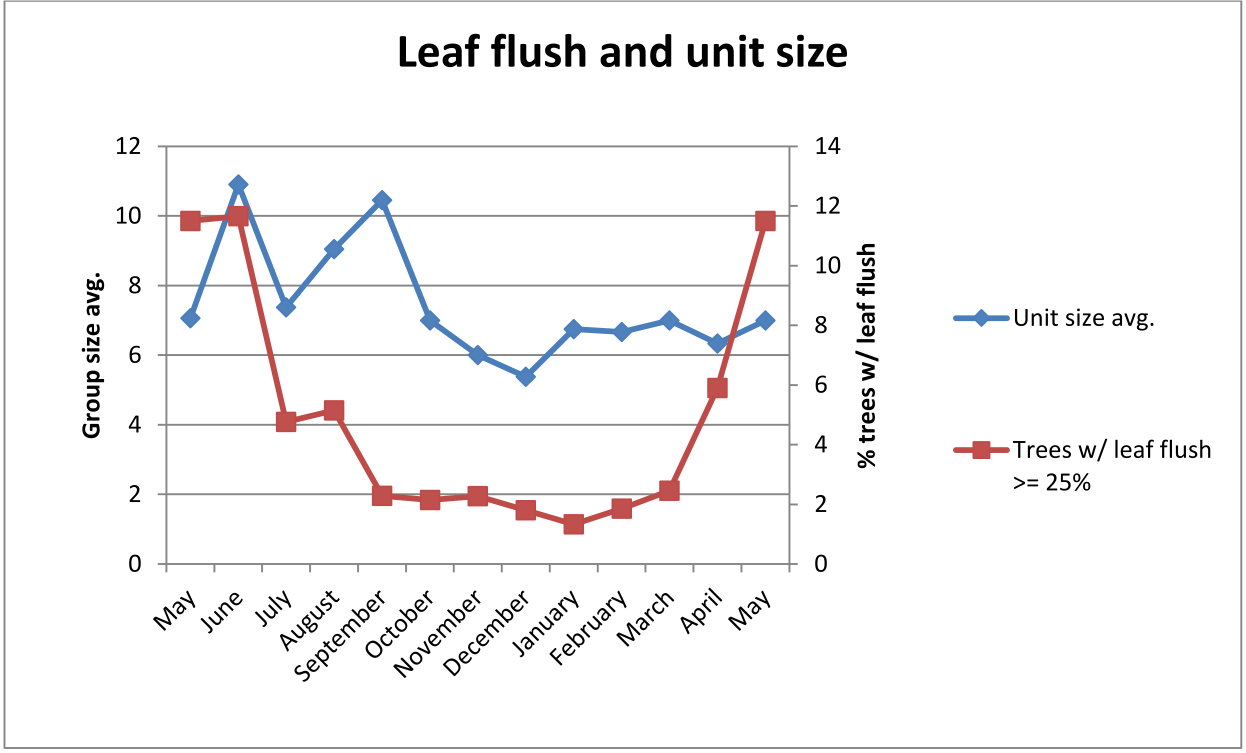


Figure 5.3. Flowering and unit size (dry season is February through May).

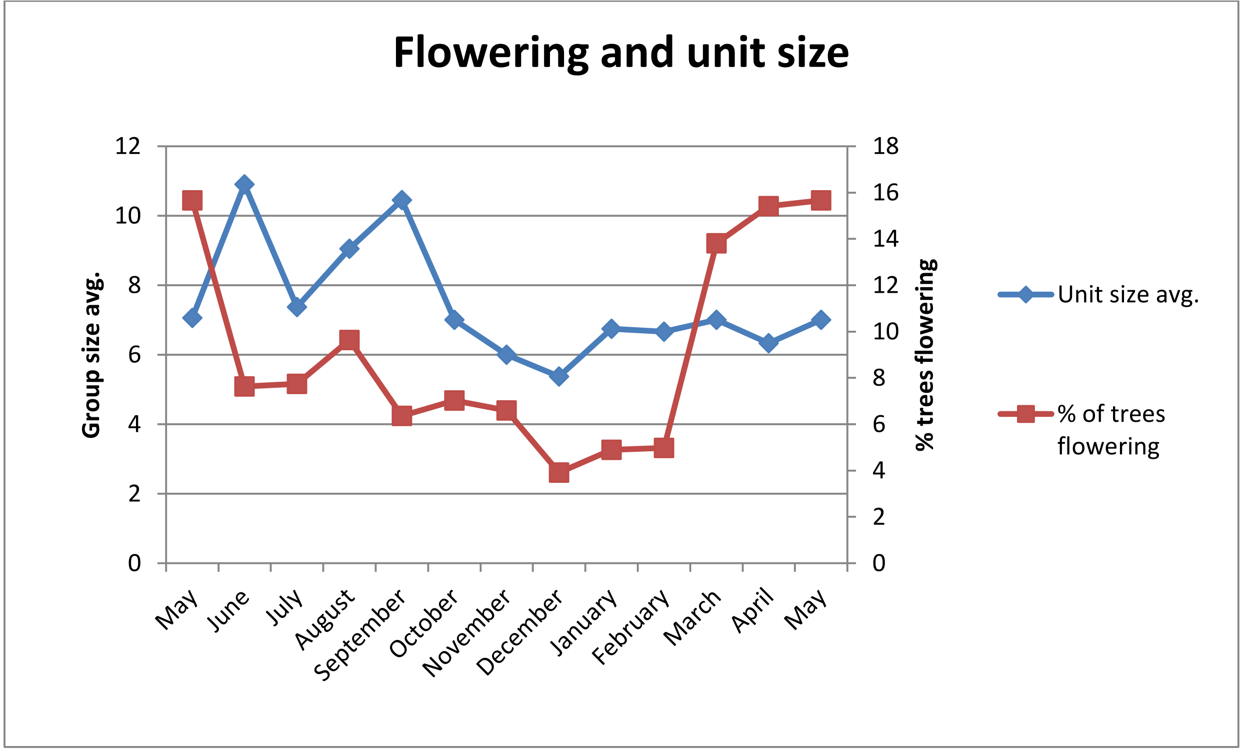


Figure 5.4. Fruiting and group size (dry season is February through May).

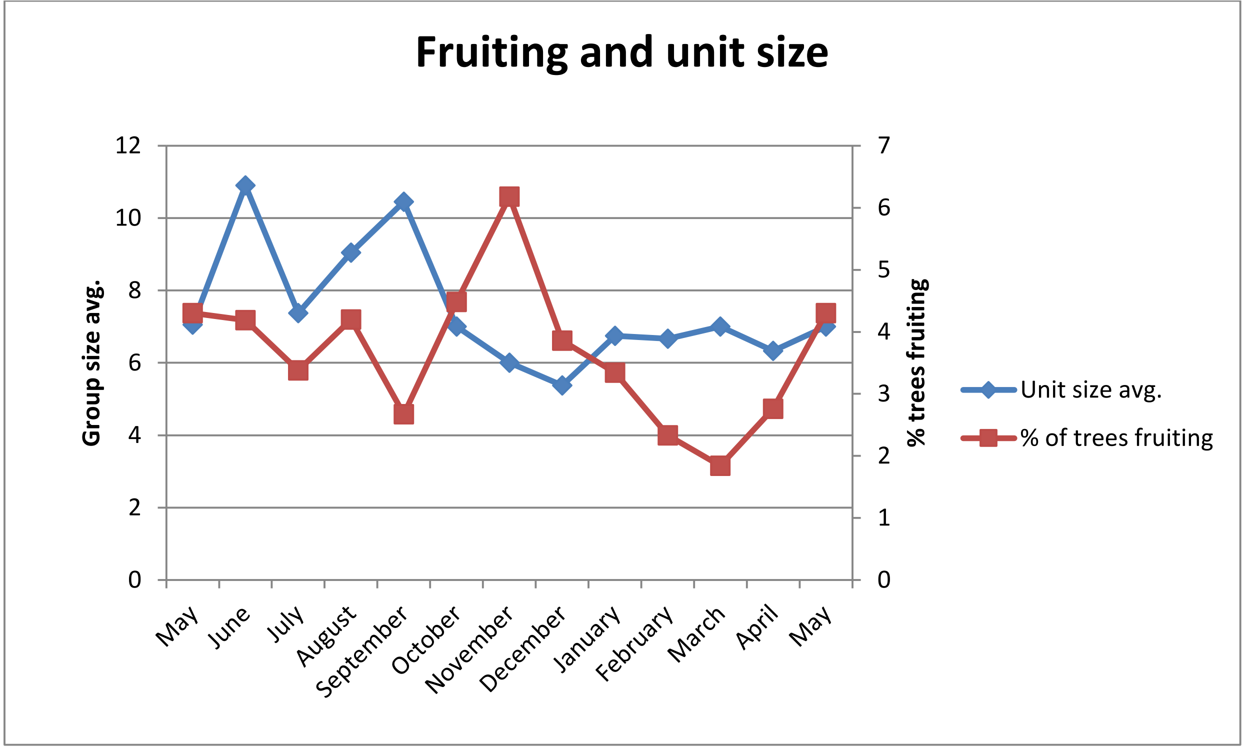


Figure 5.5. Temperature and unit size (dry season is February through May).

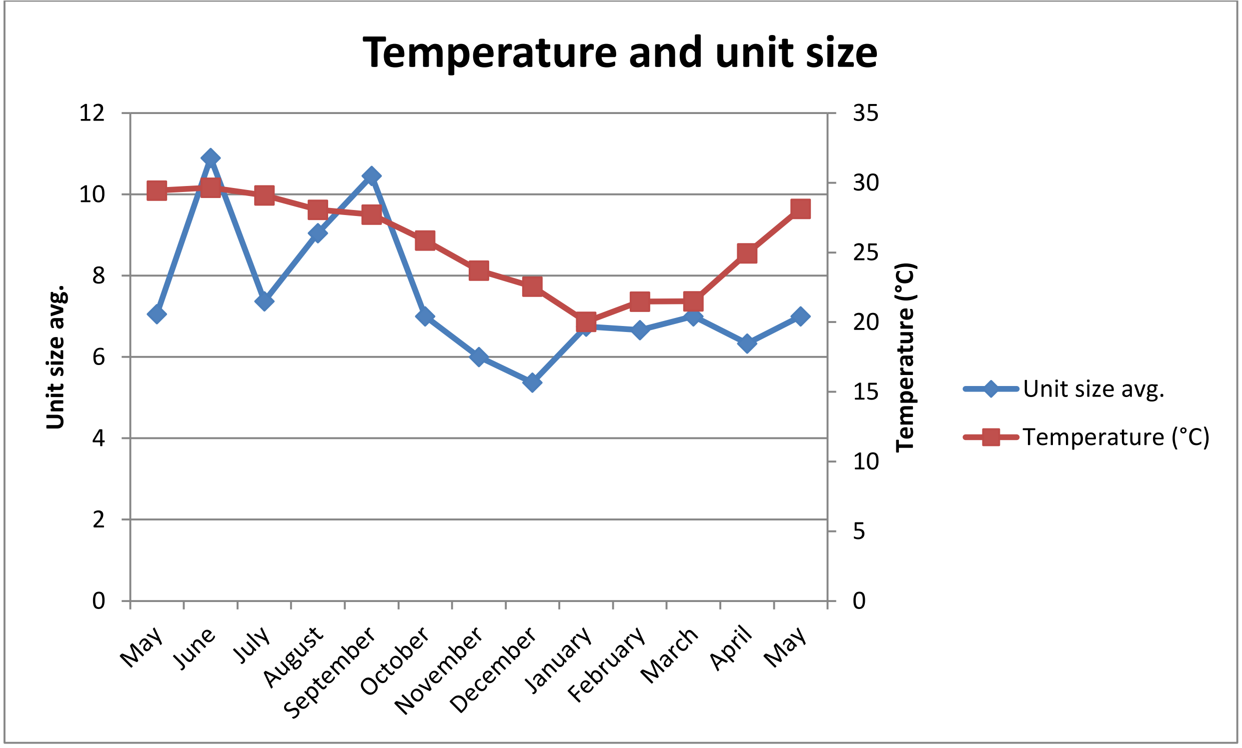
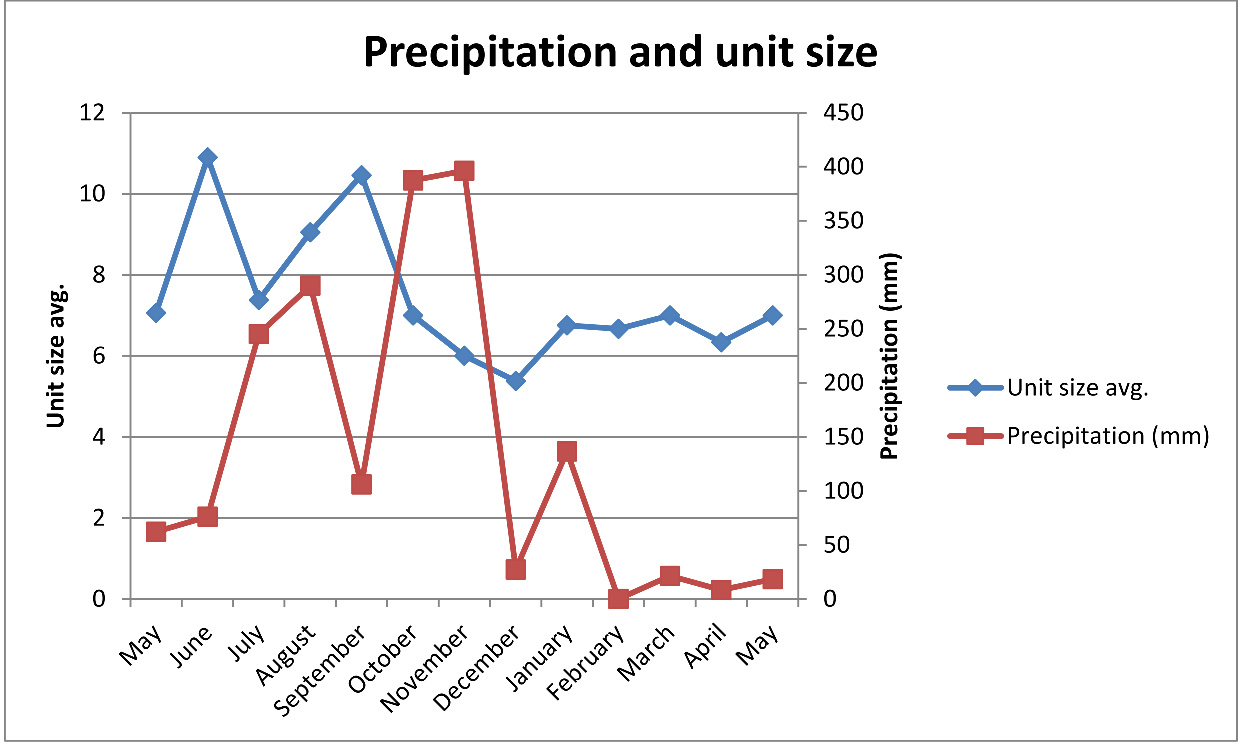


Figure 5.6. Precipitation and unit size (dry season is February through May).



5.3.2.2. Based on fission-fusion observations

This fission-fusion analysis examines only the observed fission and fusion events between units and does not include observations of super-trooping or bachelor individuals.

During research 94 separate fission-fusion events were recorded. Nearly all (n=80) of these records are from the primary research group, and although 94 records are compiled for analysis there is a bias towards the primary research group. Of the 94 fission-fusion records, 52 are fusion events and 44 are fission events.

Figure 5.7 shows that there is a peak in fission-fusion between units during the mid-wet season from October to December, and less fission-fusion during the dry and early wet season from February through September. An increase in fission-fusion events indicates the fusion of units into groups is less stable (*i.e.*, units more frequently spend time apart and there is less cohesion between units). The analysis of unit size (see Figure 5.1) shows that encounters of units were largest from May through September. The fission-fusion analysis suggests cohesion between units is greatest from February through September, as during this time groups are less likely to fissure into units.

All fission-fusion events are compiled and compared to external variables to evaluate correlations, including temperature (Figure 5.8), precipitation (Figure 5.9), leaf flush (Figure 5.10), fruiting (Figure 5.11) and flowering (Figure 5.12). Comparisons to phenology data only include data from May 2010 to May 2011 because that is when phenology data was collected. Comparisons to weather data include the weather data gathered from that month. The degree of fission and fusion are used, as opposed to only fission events or only fusion events, because fission-fusion is a daily pattern and every fission event is followed by a fusion.

The degree of fission-fusion is weakly correlated to temperature. Precipitation and fission-fusion events are significantly and positively correlated ($r\ (16) = 0.55$, $p = 0.03$). This indicates fission and fusion activities increase with increases in precipitation, or units are more consistently fused as a group during dry months.

Fission-fusion events and both fruiting and flowering are weakly correlated. Lastly, fission-fusion and leaf flush are significantly and negatively correlated ($r\ (13) = -0.54$, $p = 0.05$), indicating that when leaf flush is scarce fission and fusion activities increase, or when leaf flush is abundant units are more consistently fused.

In combination with the previous results on unit size fluctuations, these data suggest that units spent the greatest time apart during leaf flush scarcity and increases in precipitation. This does not mean group structure is seasonal, as is shown in the hourly analysis in the following paragraph. Groups are stable, but there are fluctuations in the degree of fission and fusion.

Results presented in Figure 5.13 are the percentage of time per hour which the units or groups of the 94 fission-fusion events were either fused or fissioned. These data are further compared in Figures 5.14 and 5.15 which show daily fusion and fission between the wet and dry seasons.

It is interesting to note that all observations of fission-fusion events in the morning before the group had awaken, and in the evening as the group was preparing for sleep, recorded units in a fused state. This means that units, regardless of season or factors relating to differences in degree of fission and fusion, always slept together as a group every day.

During a typical day there is an increase in fission in the morning between 6:00 and 10:00, then an increase in fusion around 10:00 to 11:00, followed by a second increase in fission in the early afternoon, and fusion again in the late afternoon or early evening before sleeping. This pattern correlates significantly with the average daily activity budget of doucs, reported and discussed in Chapter 6. Wet and dry seasons are overall very similar, although there is slightly more fusion and less fission in the dry season than in the wet season. However, comparing the percentage of time fissioned or fused at each hour interval between the wet and dry seasons with the nonparametric two-tailed Mann-Whitney U test shows that this difference is statistically significant regarding fusion between wet and dry seasons (U=143, p=0.04, $n_{\text{wet, dry}}$ = 14, 14) but not fission (U=130.5, p=0.14, $n_{\text{wet, dry}}$ = 14, 14). This indicates units in the dry season spend a greater amount of daily time in a fused state, and groups most frequently fission into units when precipitation increases and leaf flush is scarce.

Figure 5.7. Number of fission-fusion events per month (dry season is February through May).

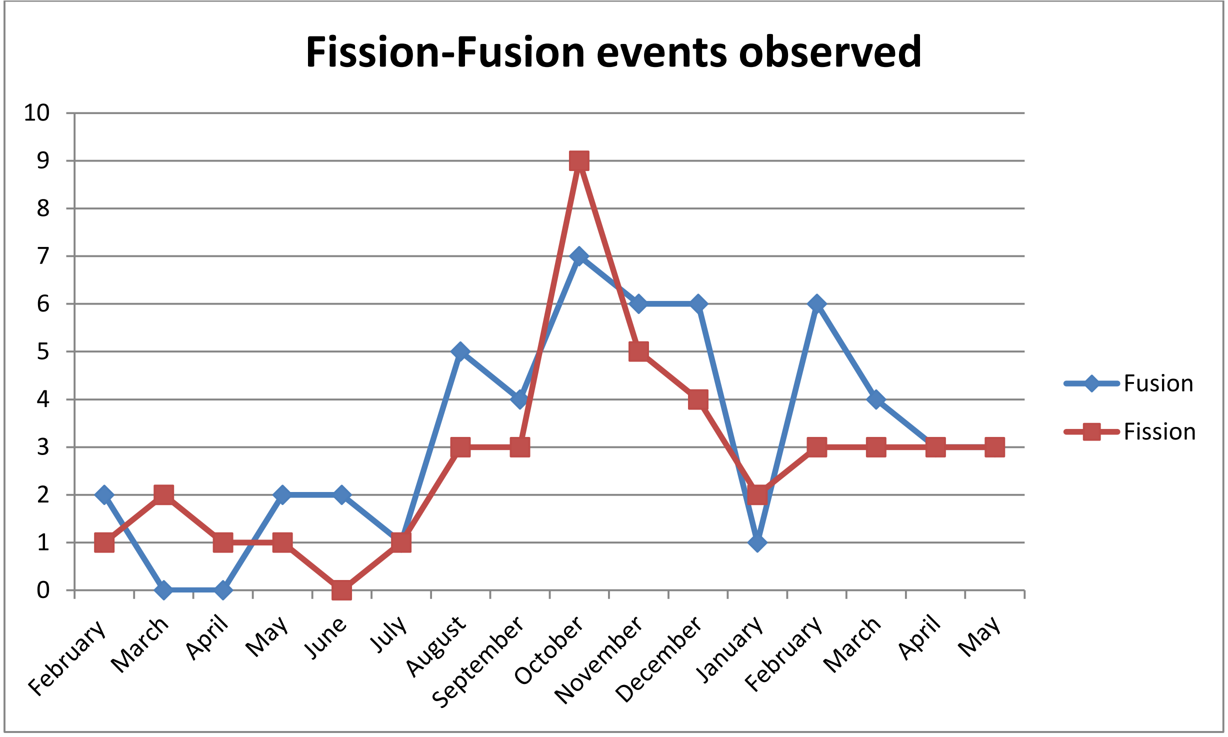


Figure 5.8. Number of fission-fusion events and temperature.

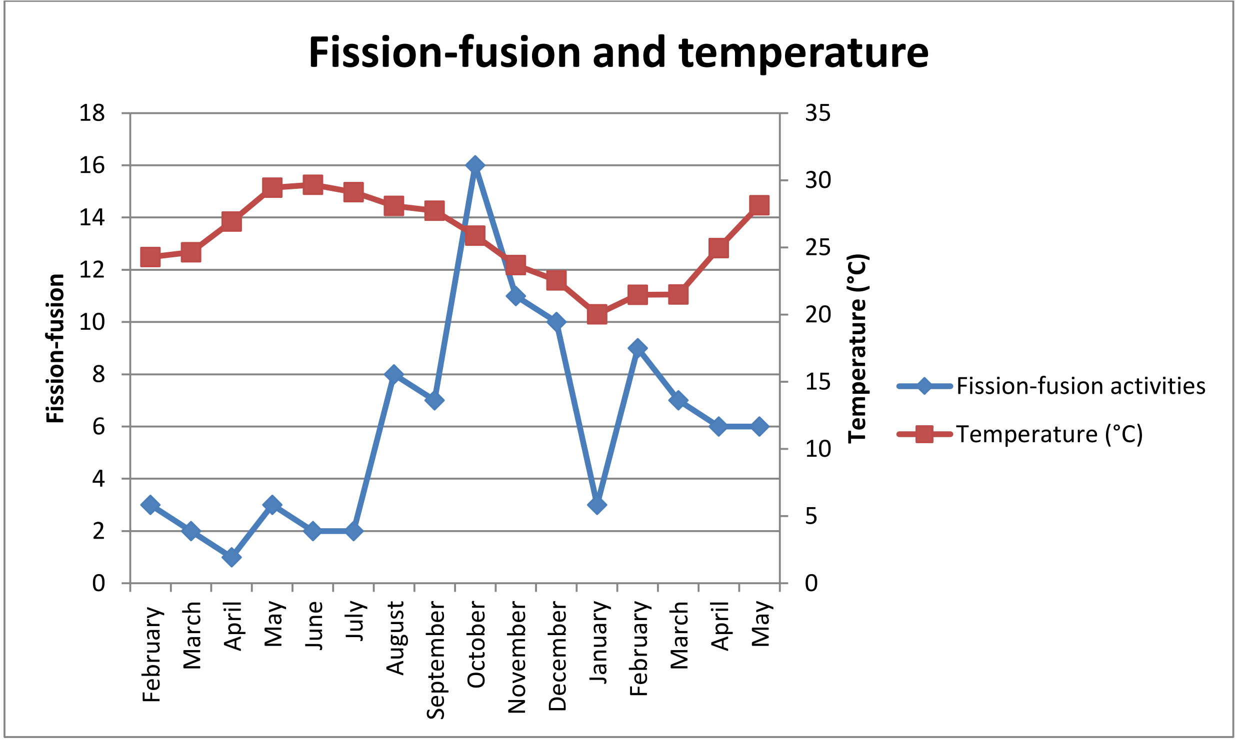


Figure 5.9. Number of fission-fusion events and precipitation.

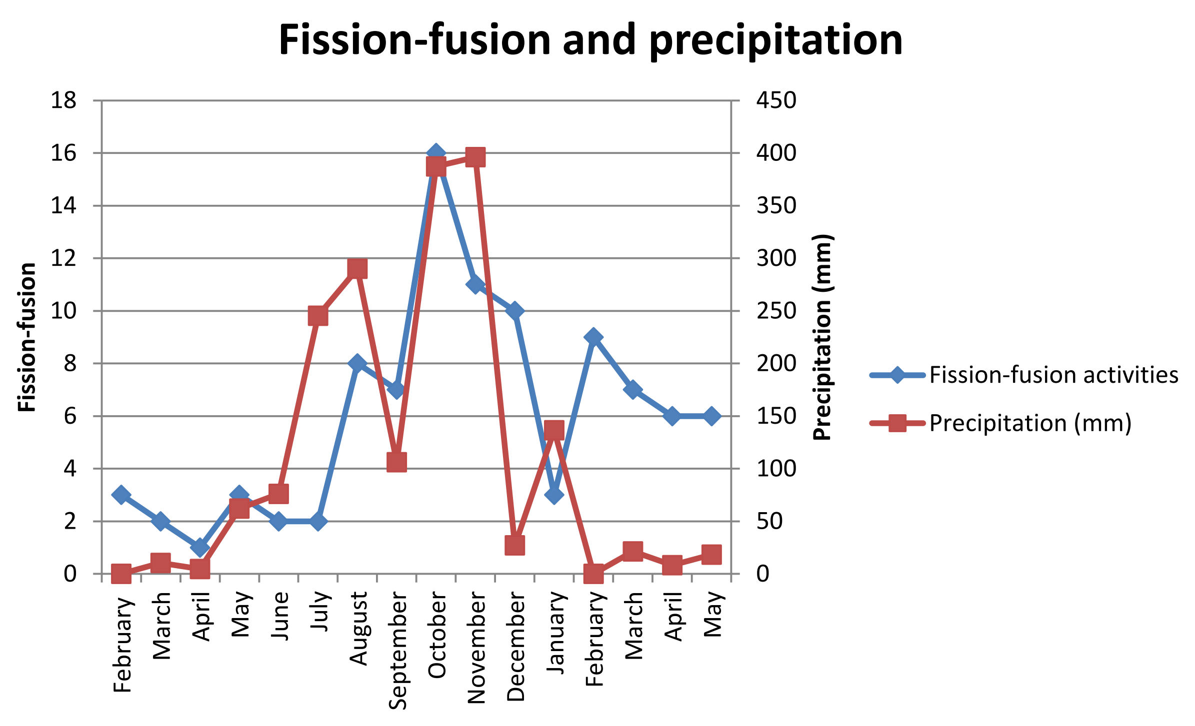


Figure 5.10. Number of fission-fusion events and leaf flush (dry season=February through May).

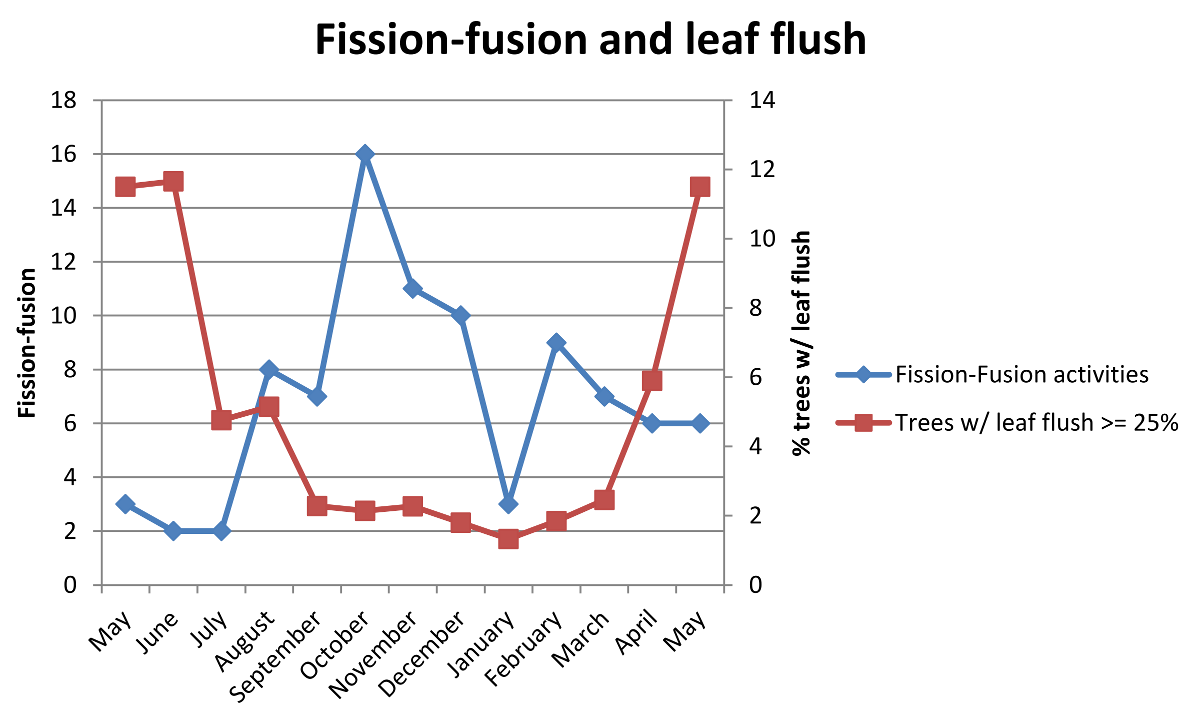


Figure 5.11. Number of fission-fusion events and fruiting (dry season=February through May).

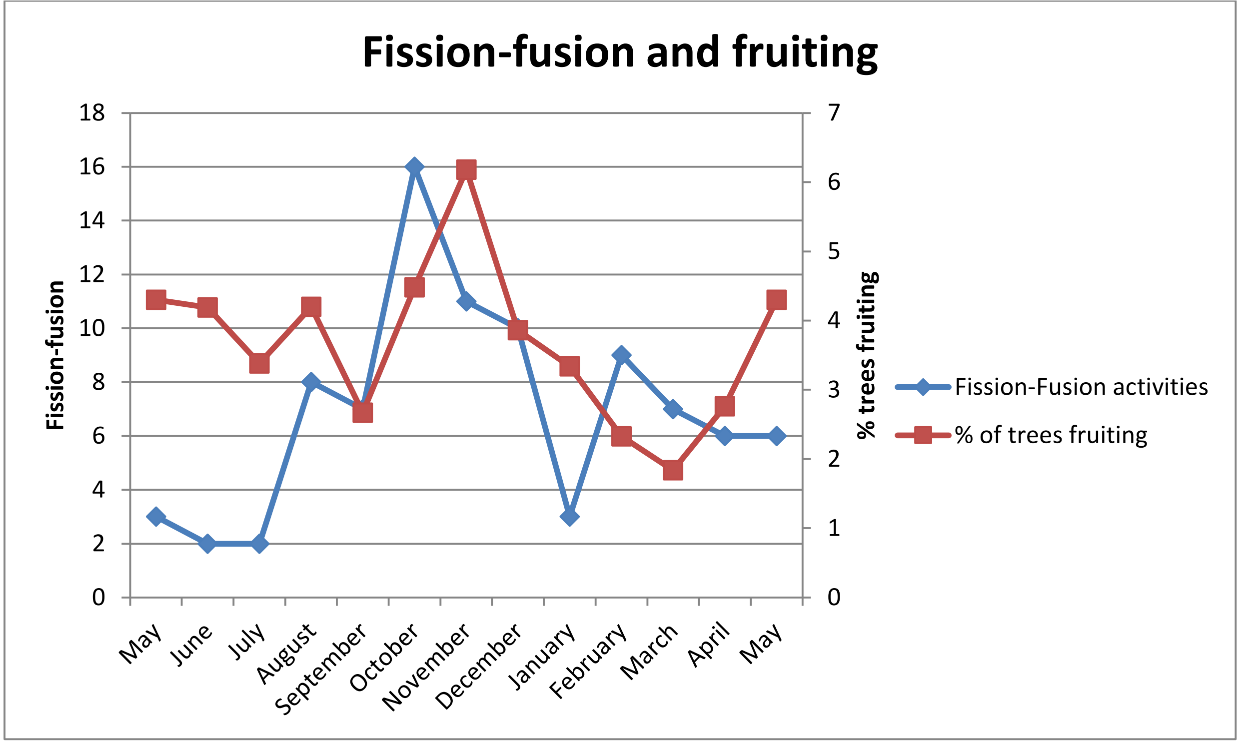


Figure 5.12. Number of fission-fusion events and flowering (dry season=February through May).

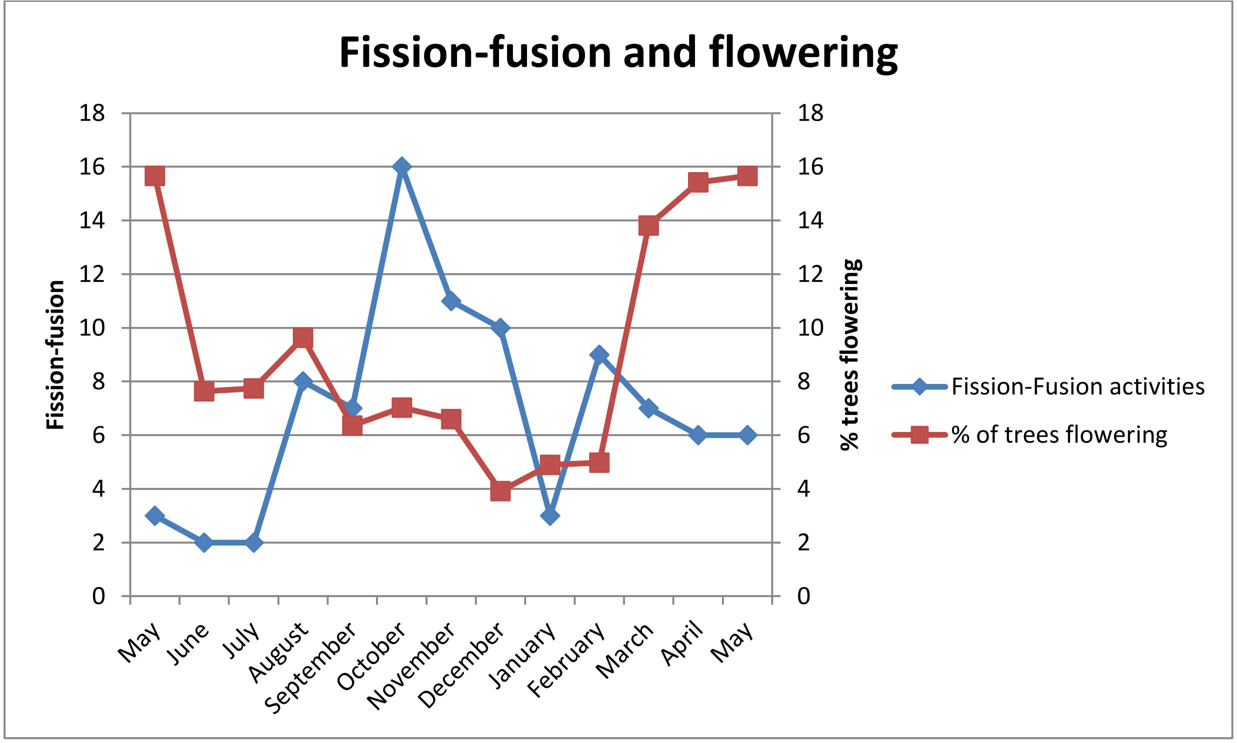


Figure 5.13. Fusion and fission over an average day.

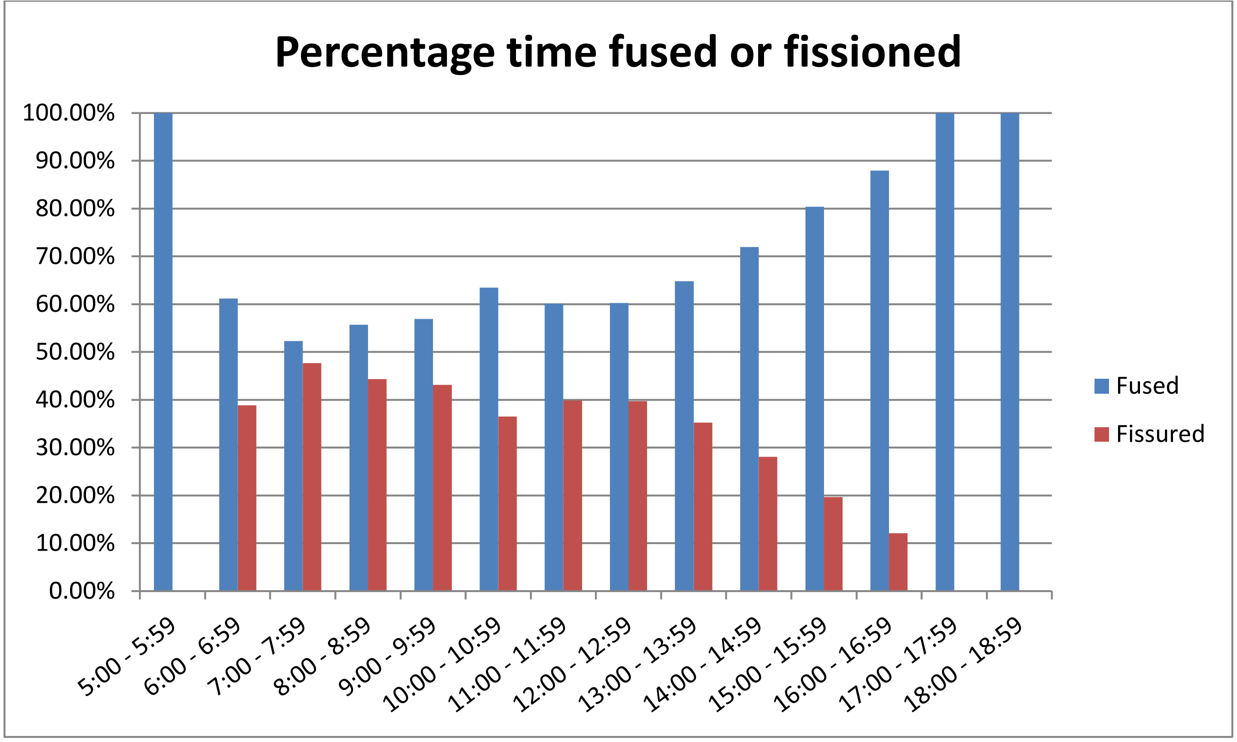


Figure 5.14. Fusion compared over an average wet and dry season day.

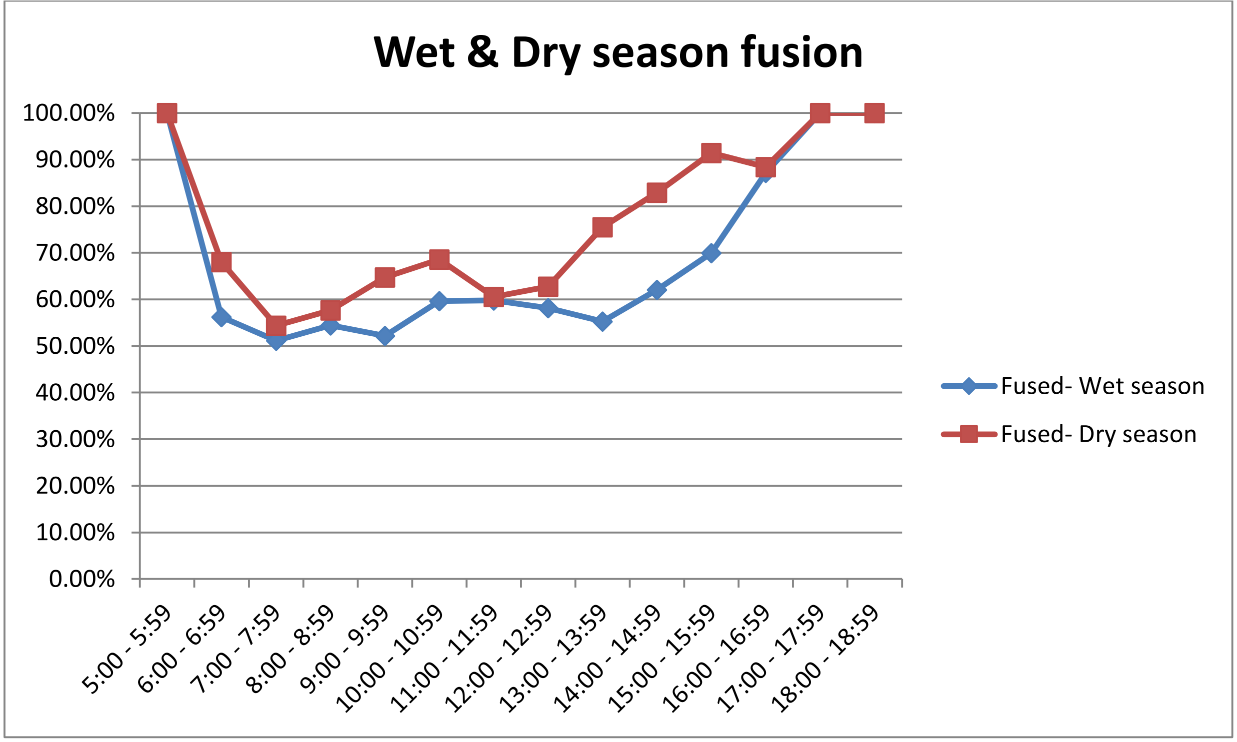
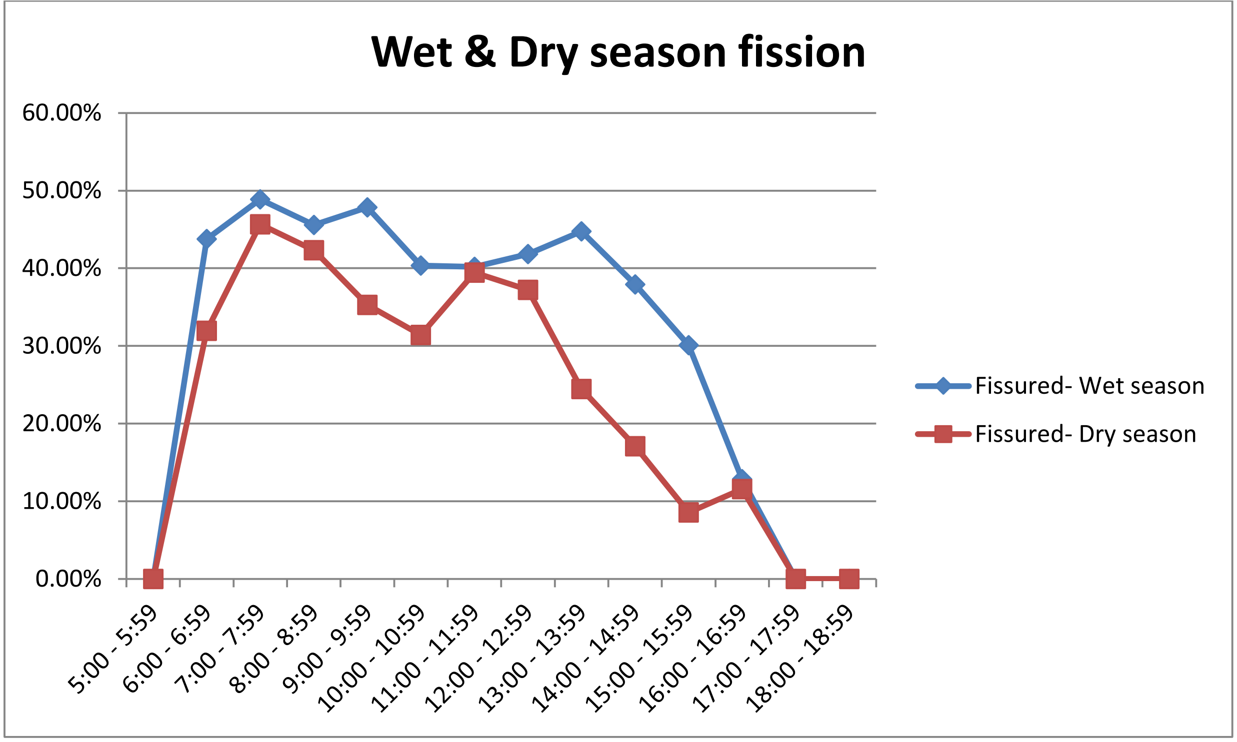


Figure 5.15. Fission compared over an average wet and dry season day.



5.3.3. Ranging

5.3.3.1. Home range and core area

The home range of the three main research groups was assessed, but only the home range of the primary research group was determined with enough certainty to allow detailed analysis. Therefore, only data on the home range of the primary research group is presented. This analysis is based on 592 GPS marks. Their home range comprised 36.001 ha based on minimum convex polygon analysis, and the core area comprised 8.02 ha calculated by 50% kernel density analysis. Figures 5.16 and 5.17 illustrate the location of the home range of the primary research group on different map scales. Their home range includes part of a large stream which is one of the largest on Son Tra and has water throughout the year. This water source may impact their home range size and ranging behaviors.

There is seasonal variation in the use of home range. Figure 5.18 illustrates the wet and dry season ranging variability using minimum convex polygon analysis. The dry season contains 202 GPS marks and comprises 23.65 ha. The wet season contains nearly double the marks (and double the months) with 390 GPS marks, comprising 32.95 ha.

GPS marks are divided by month allowing the calculation of the ranging variation each month. Exceptions are June and July which had low numbers of GPS marks and therefore both months are combined into one for an 11 month comparison. Figure 5.19 illustrates monthly ranging variation, and Figure 5.20 graphs the change over time. For graphing purposes, the months of June and July are separated and the range of both months represents the minimum polygon area when combined. Monthly ranging variation does not follow the seasonal pattern.

Monthly ranging variation was compared to weather and phenology data. As before, June and July are retained as separate months for these analyses although each represents the combined GPS data. Home range and precipitation (Figure 5.21), temperature (Figure 5.22), leaf flush (Figure 5.23), flowering (Figure 5.24) and fruiting (Figure 5.25) are compared for significant correlations.

Seasonal variation in ranging (see Figure 5.18) suggests a correlation between home range and precipitation or home range and fruiting. However analyzing the data on a monthly scale illustrates a more complex pattern (see Figure 5.19). Pearson’s Correlation shows that precipitation and temperature are only weakly correlated to ranging variation. Similarly, there are non-significant weak correlations between ranging and leaf flush, flowering, and fruiting. Variation in ranging is also weakly correlated with the degree of monthly fission-fusion events, indicating monthly ranging variation does not relate to the degree of unit cohesion.

Ranging behavior does not need to fluctuate depending on a single weather or phenology variable. Additionally, February is the driest month and the month with the most activity along the stream (see Figure 5.19). An increase in February ranging may be related to water intake.

The two main conclusions are that on a seasonal scale the doucs used a greater amount of their home range during the wet season, similar to other *Pygathrix* studies, and on a monthly scale ranging analysis is not correlated with availability of food items or weather data.

Figure 5.16. GPS marks for home range of the primary research group.

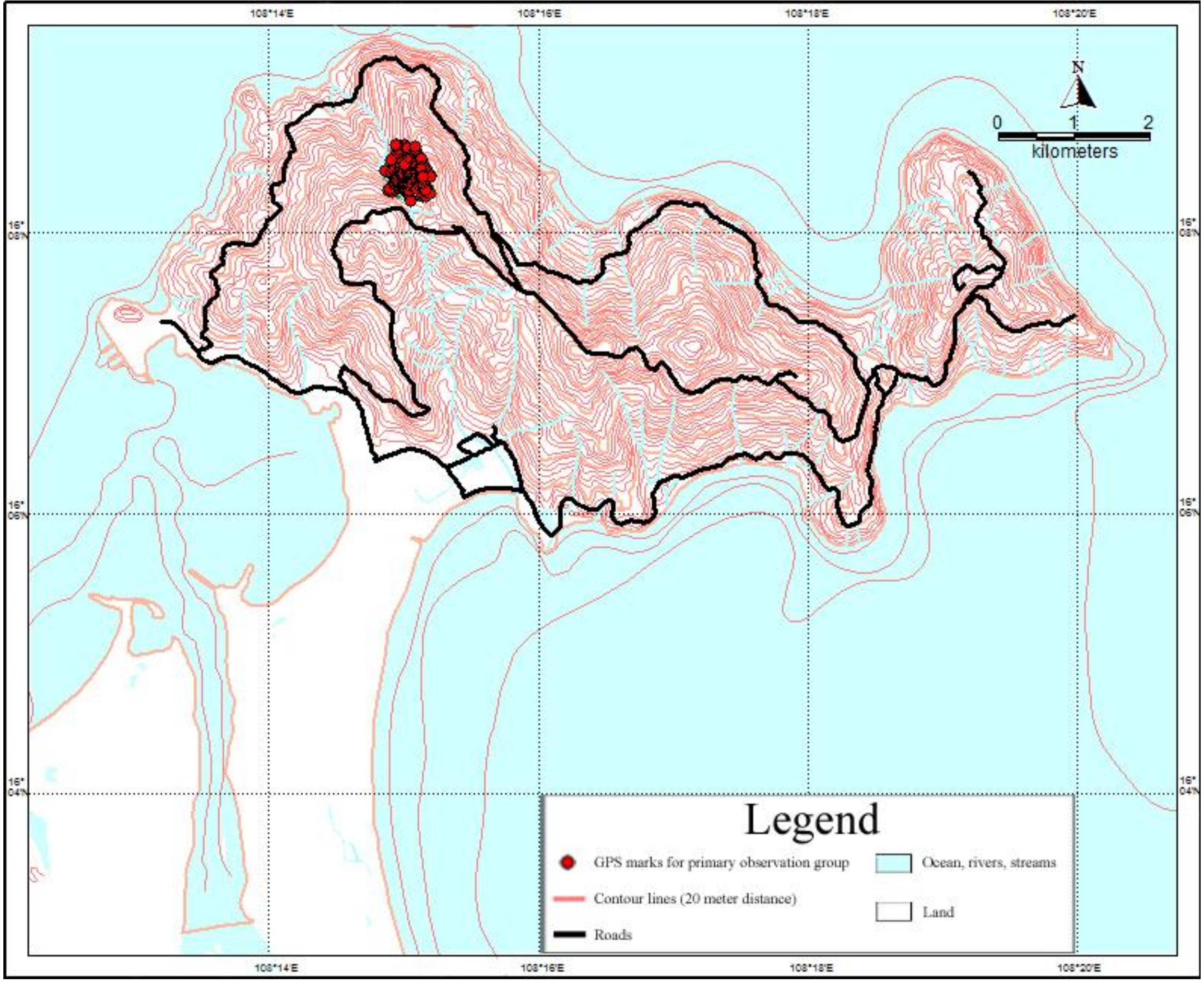


Figure 5.17. Home range and core area of the primary research group.

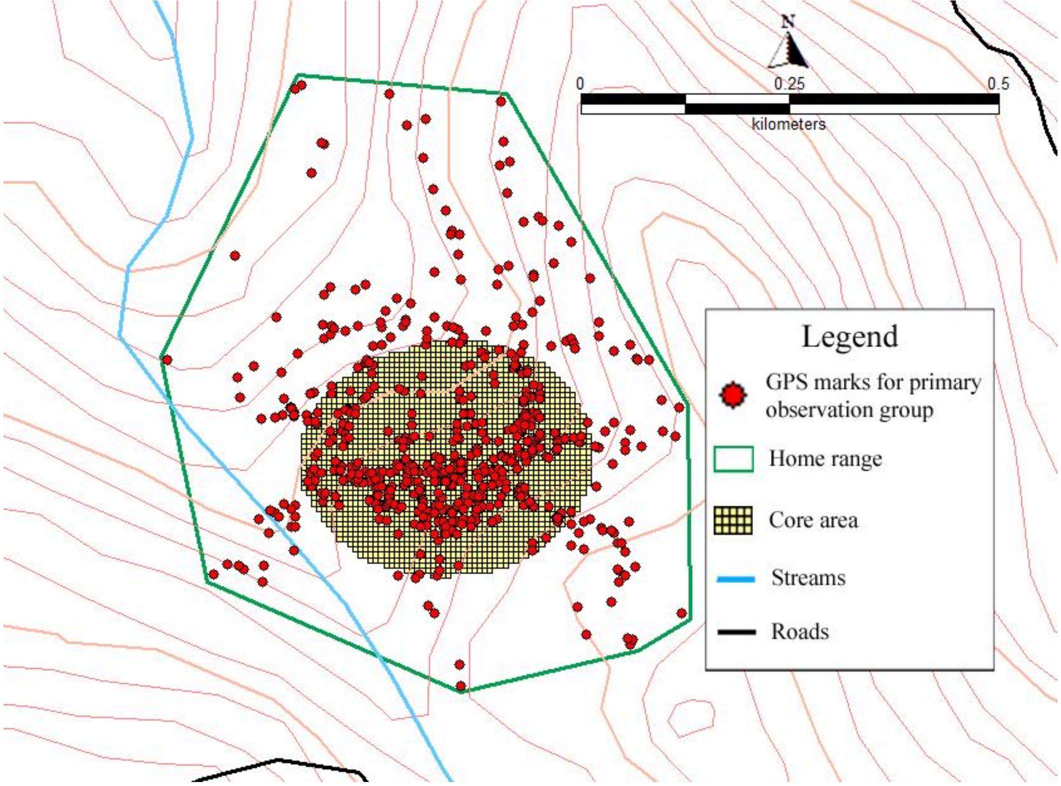


Figure 5.18. Seasonal variation in range use.

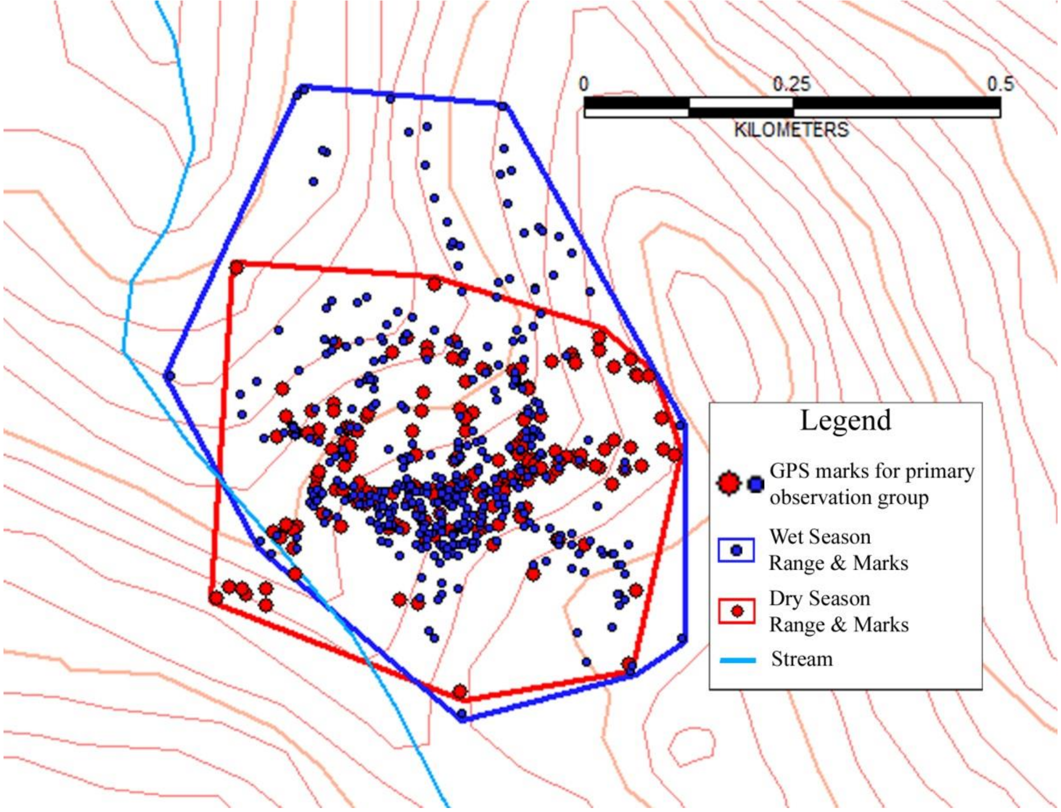


Figure 5.19. Monthly range use variation by the primary research group.
A minimum convex polygon is used to illustrate the location of the core area (dry season=February through May).

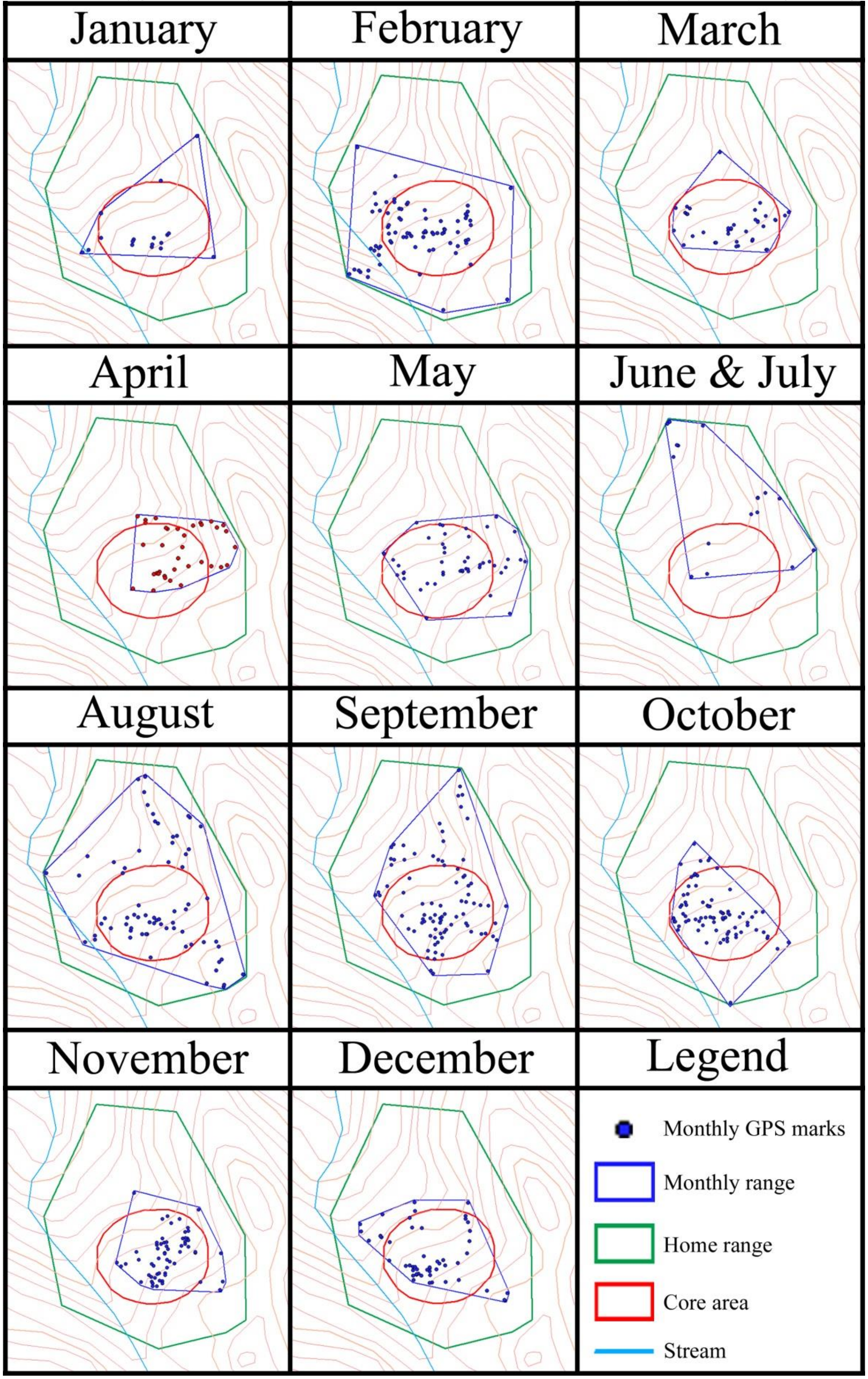


Figure 5.20. Monthly range use variation.
Number of GPS marks in brackets (N) (dry season=February through May).

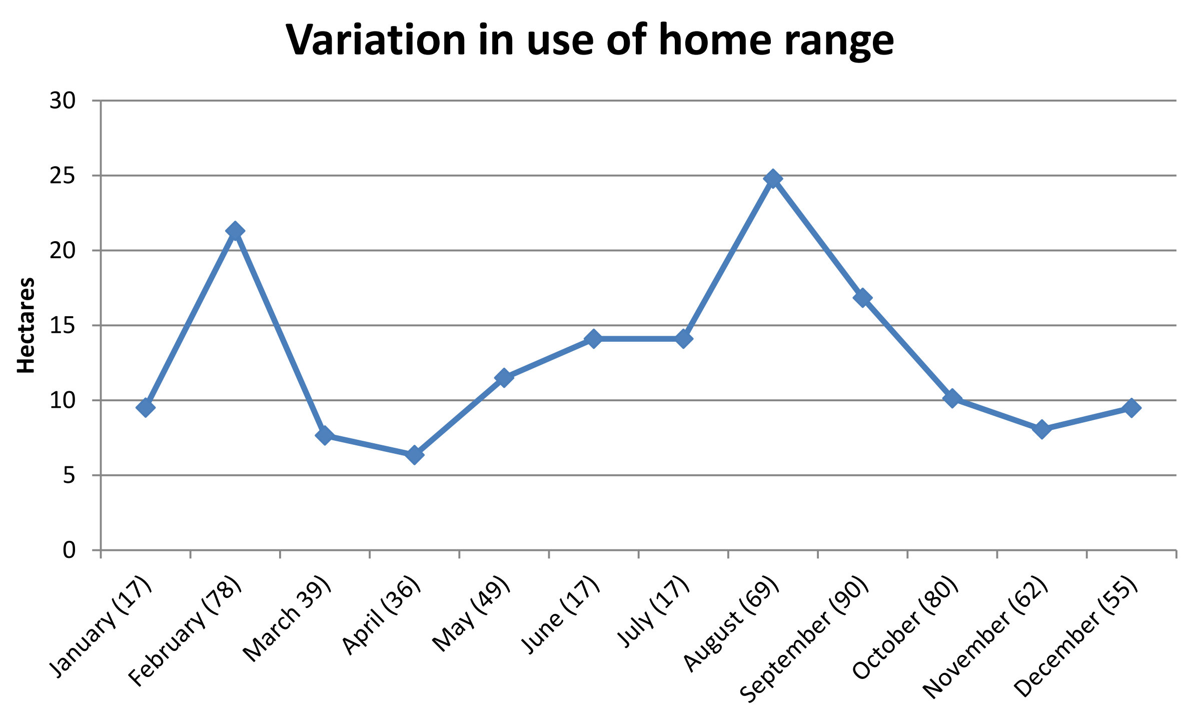


Figure 5.21. Monthly range use variation and precipitation (dry season=February through May).

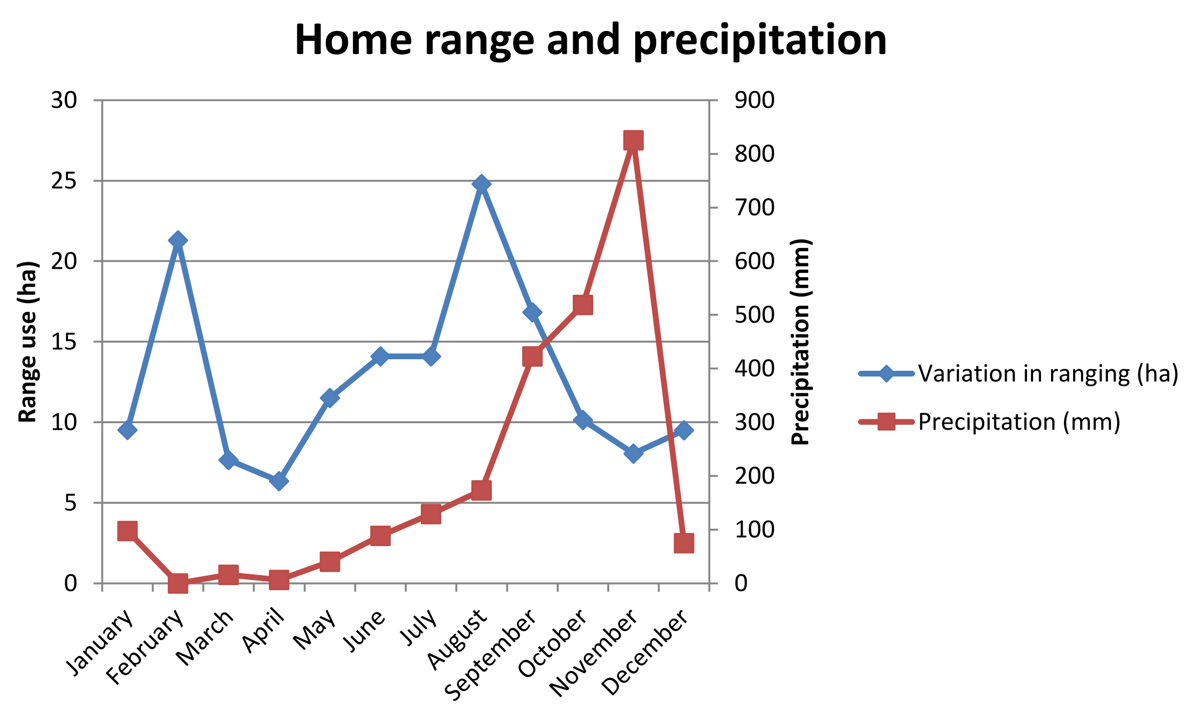


Figure 5.22. Monthly range use variation and temperature (dry season=February through May).

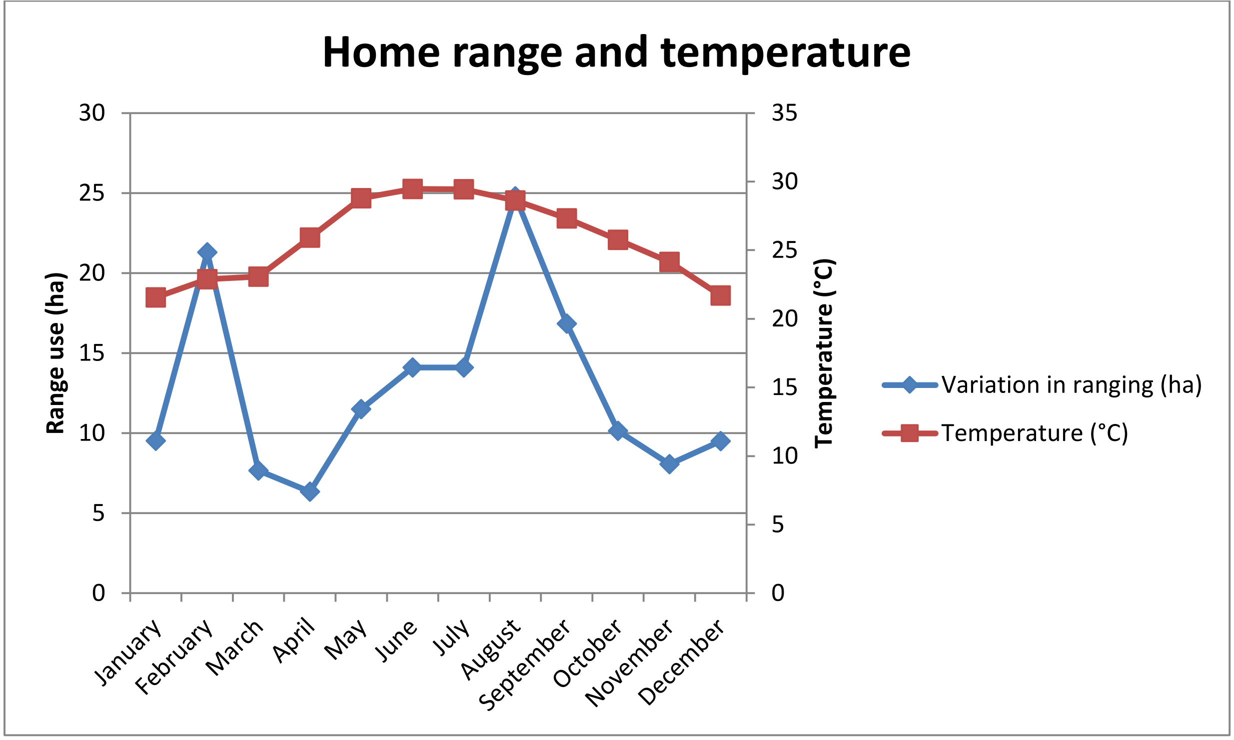


Figure 5.23. Monthly range use variation and leaf flush (dry season=February through May).

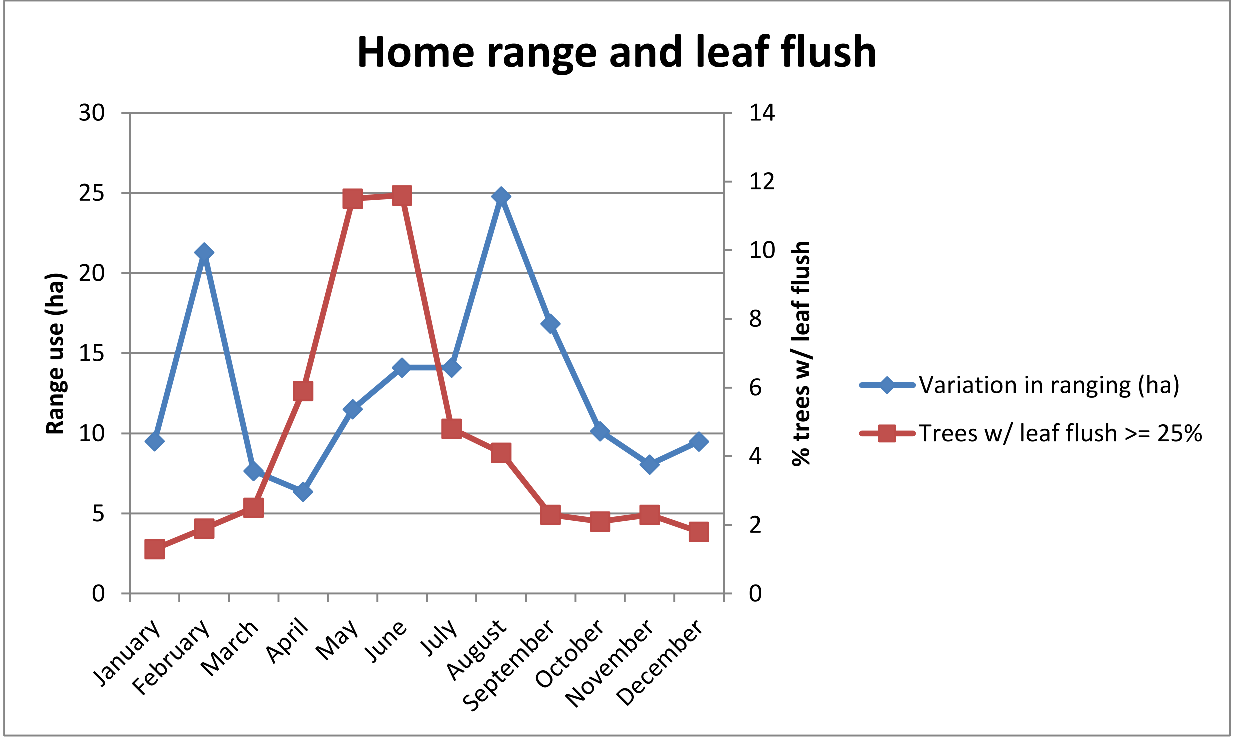


Figure 5.24. Monthly range use variation and flowering (dry season=February through May).

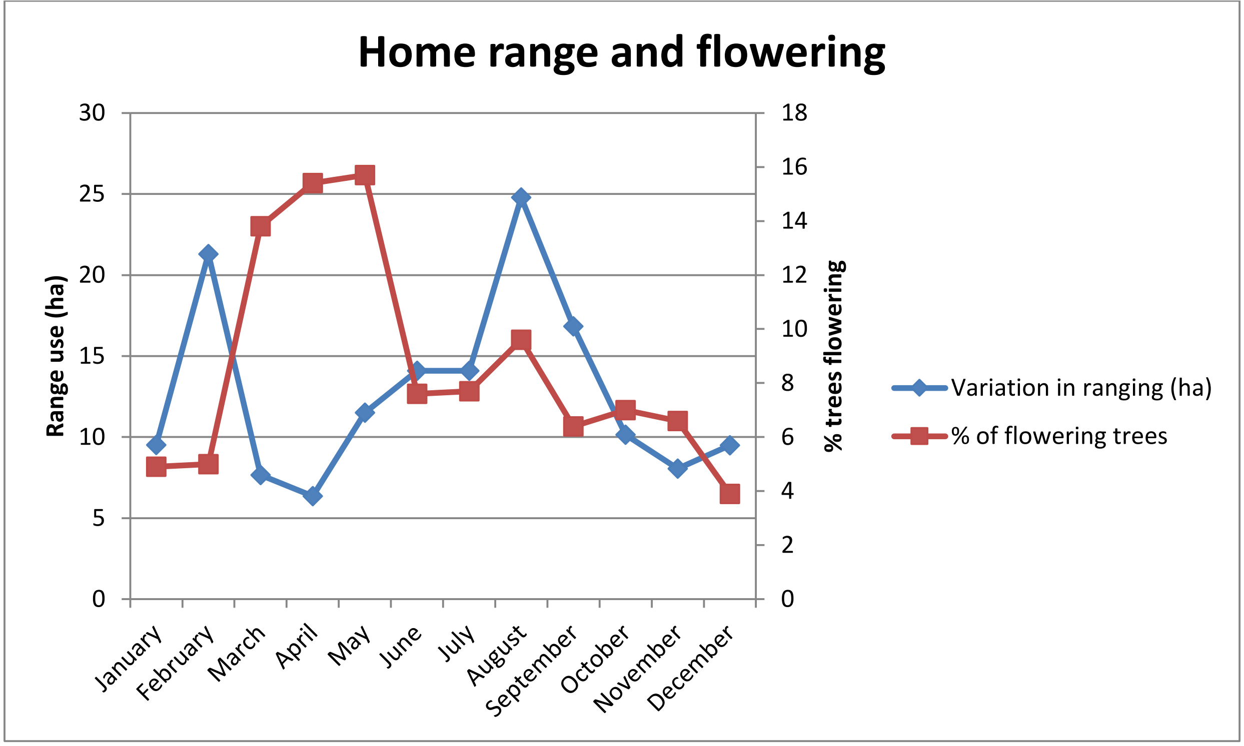


Figure 5.25. Monthly range use variation and fruiting (dry season=February through May).

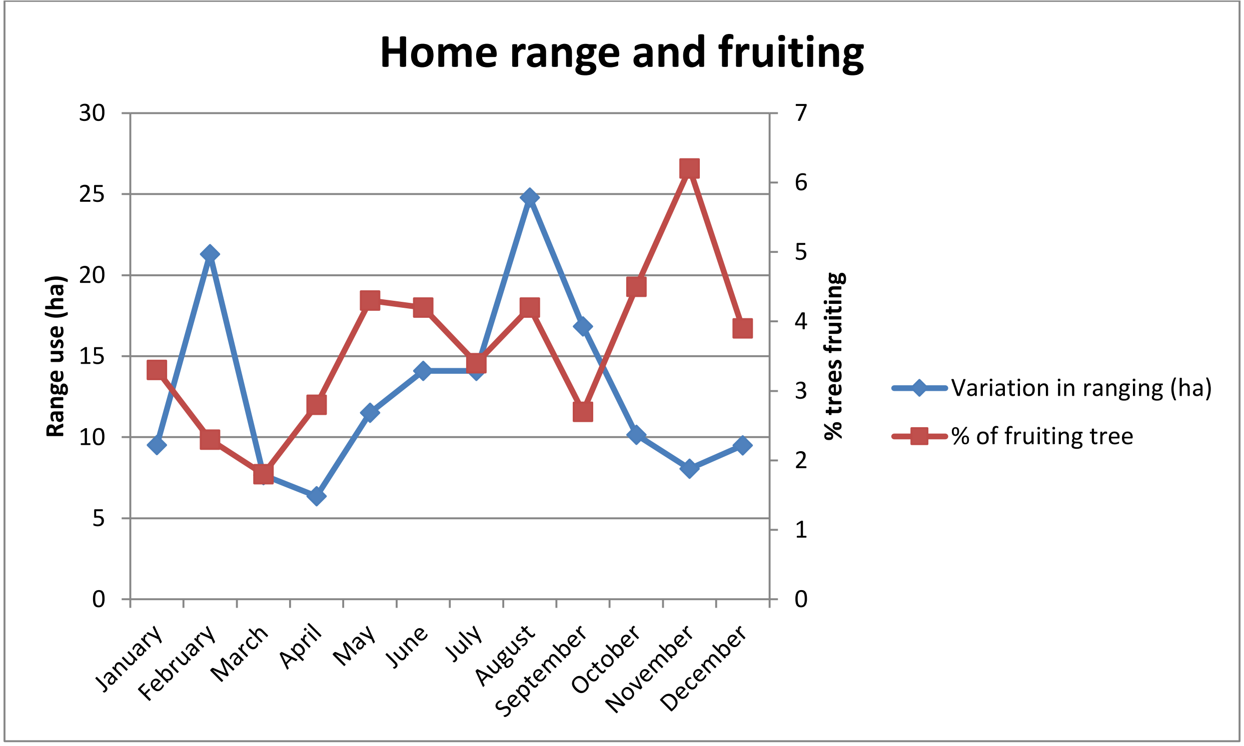
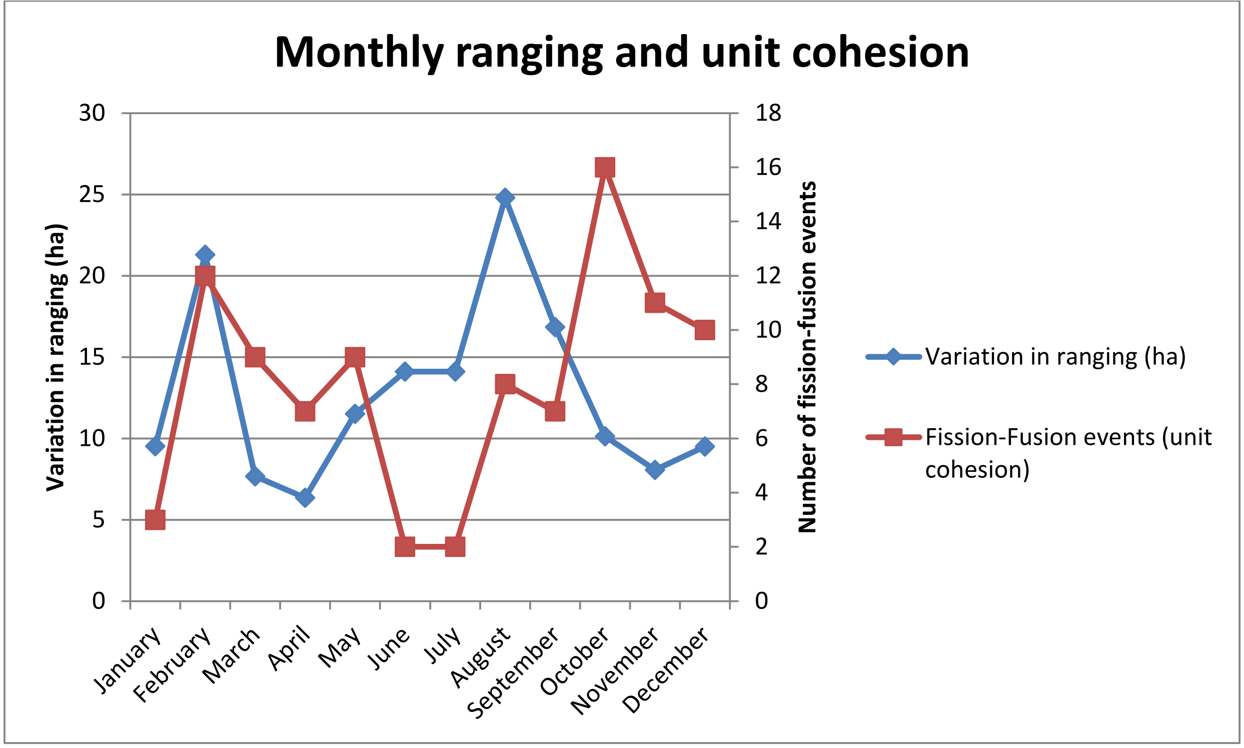


Figure 5.26. Monthly range use variation and degree of unit cohesion (fission-fusion events).

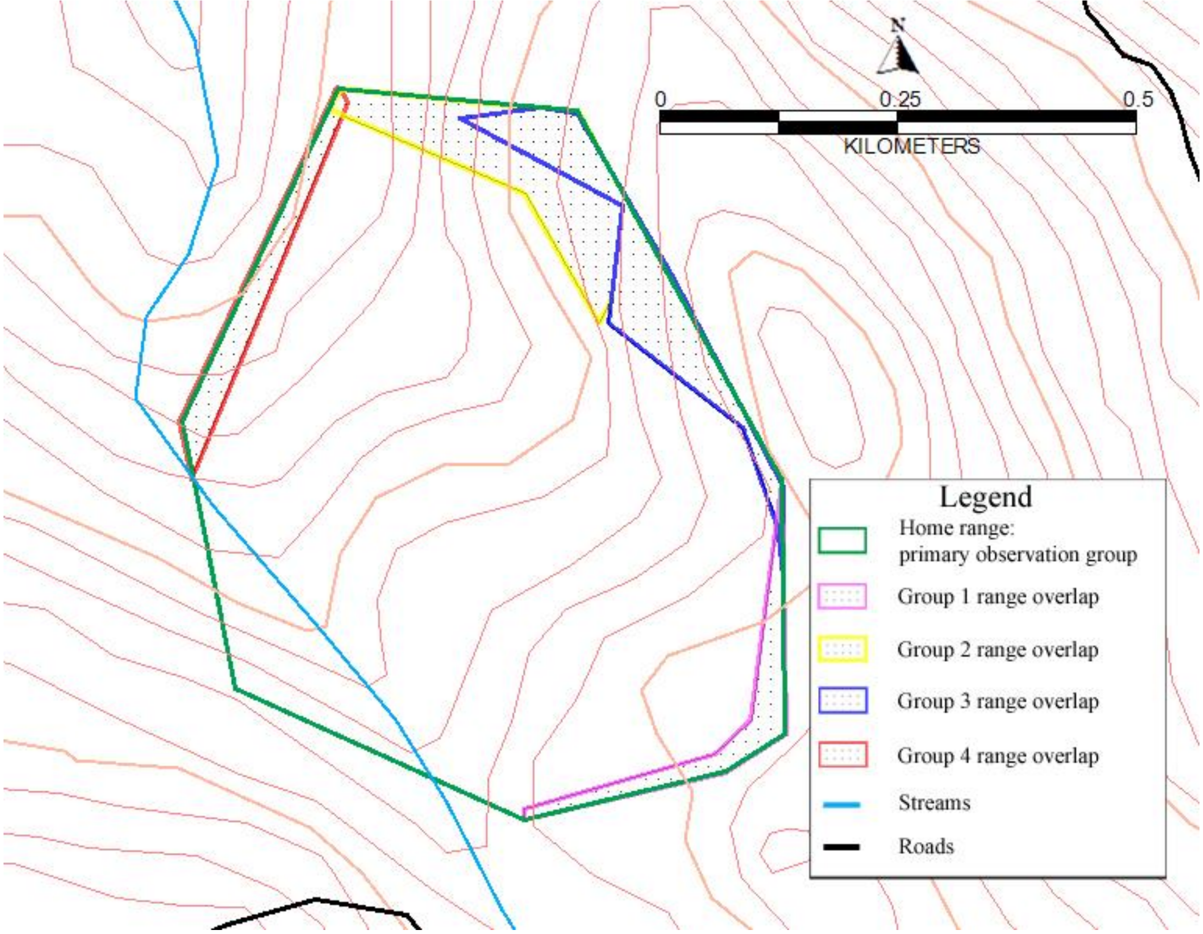


5.3.3.2. Degree of overlap between adjacent home ranges

There were at least four groups adjacent to the primary research group (Figure 5.27). All adjacent groups were only encountered along the borders of the home range of the primary research group, and when the primary group was also near the borders. This gives the impression of minimal home range overlap, although the degree of overlap cannot be stated for certain because the home ranges of adjacent groups were not analyzed.

I frequently encountered the group to the southeast (Group 1) and the group to the west (Group 4) of the primary research group's home range. Their home ranges may only have minimal overlap with the primary research group's home range (1.03 and 1.11 ha, respectively). The groups to the northeast (Group 2) and north (Group 3) may comprise multiple units of the same group or represent separate groups as assumed here. The home range of Group 2 appears to have notable overlap with the home range of the primary research group (2.07 ha), and with the home range of Group 3. Group 3 was less frequently encountered but its home range might have the highest degree of overlap with the home range of the primary research group (2.76 ha). Group 2 and the primary research group would occasionally pass by or sleep near each other along the borders of their home range (within 50 m) without displaying any aggressive behaviors or alarm calling. No douc group appeared to occupy the area to the southwest of the primary research group's home range, which may be related to a road running along the top of the slope. As there appears to be some degree of overlap between the home ranges of each adjacent groups, the total amount of potential overlapping home range between the primary research group and all adjacent groups was 5.8 ha. Again, this estimate is based on the location of encounters with adjacent groups, not on an analysis of the home range of adjacent groups.

Figure 5.27. Home range overlap.



5.3.3.3. Daily path lengths

During this study, 17 full-day follows were successful. This number is low in comparison to other colobine studies (*Pygathrix* studies excluded) indicating the difficulty of habituating doucs and the frequency with which the primary research group became agitated when being followed as the day progressed. As described in Chapter 3, the comfort of the doucs was given precedence over data collection.

All full-day follows were with the primary research group. There is at least one full day follow to represent each month from August 2010 through May 2011, except for January. The average daily path length was 509.11 ± 244.87 m, ranging from 136.86 to 987.25 m. The average dry season daily path length was 595.01 ± 293.6 m, and the average wet season daily path length was 432.75 ± 155.72 m. Daily path lengths vary greatly within seasons and months.

Daily path lengths are evaluated on daily and monthly scales. At the daily scale, path lengths are compared to daily data for temperature and precipitation. Path lengths are not compared to phenology data at the daily scale because phenology data was not recorded on a daily basis. At the monthly scale, path lengths are compared to the data for temperature, precipitation, and phenology.

Figure 5.28 and 5.29 illustrate the scatterplot for daily path lengths and weather. Pearson's Correlation coefficient reveals a weak correlation between daily path lengths and temperature, but a significant correlation between path lengths and daily precipitation ($r(17) = 0.52$, $p = 0.03$), indicating daily path lengths are significantly influenced by rainfall.

Correlations between daily path lengths and leaf flush (Figure 5.30), flowering (Figure 5.31), fruiting (Figure 5.32), and the degree of unit cohesion (Figure 5.33) are all non-significant and weak.

Table 5.1. Daily path lengths of the primary research group.

	Aug. 2010	Sept. 2010	Oct. 2010	Nov. 2010	Dec. 2010	Feb. 2011	Mar. 2011	Apr. 2011	May 2011
Day range 1	518.16	743.1	482.19	335.28	342.29	561.14	585.83	732.13	136.86
Day range 2		607.77	320.96	270.36		768.4	136.86		987.25
Day range 3			274.63			851.61			

Figure 5.28. Daily path lengths and daily temperature, with line of best fit.

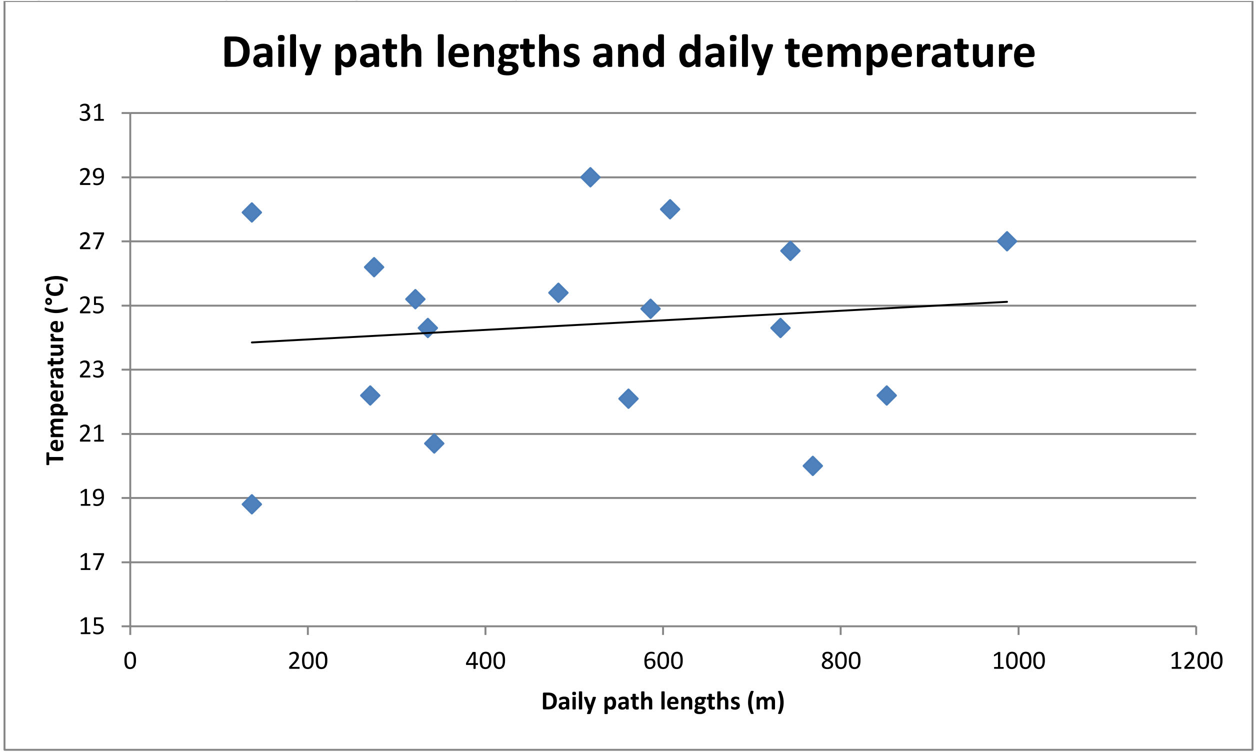


Figure 5.29. Daily path lengths and daily precipitation, with line of best fit.

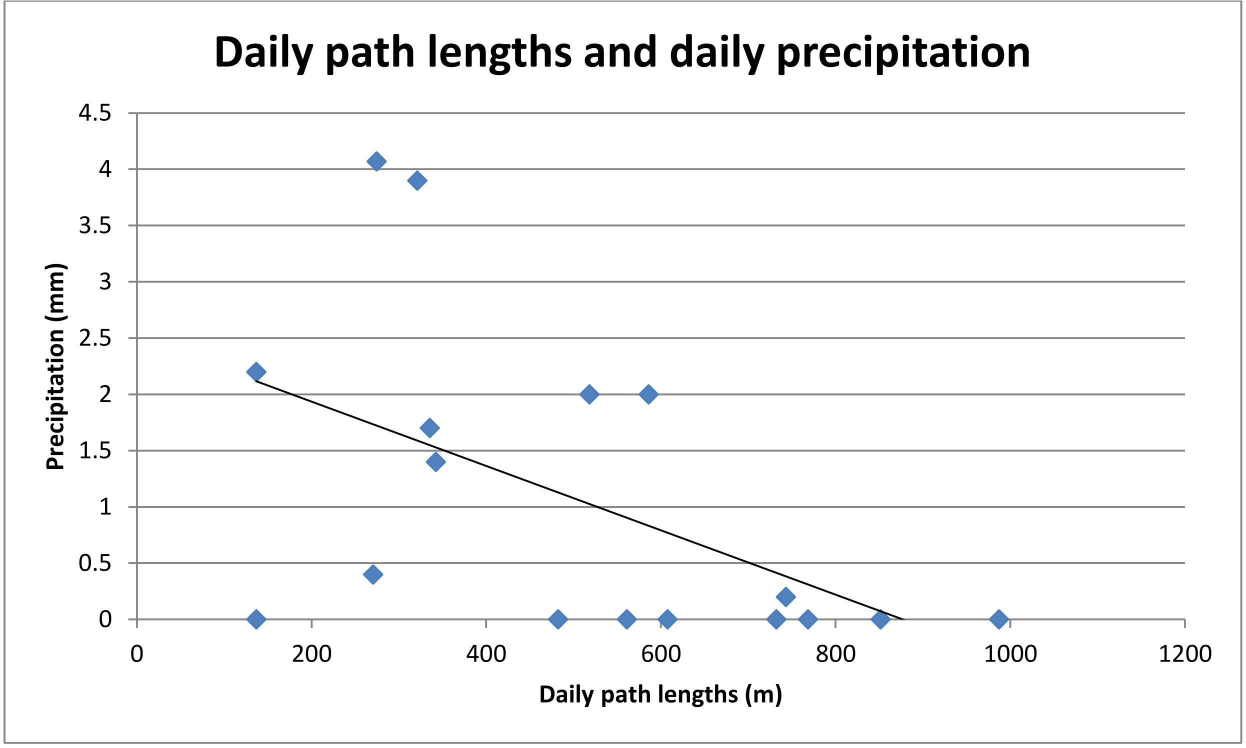


Figure 5.30. Daily path lengths and leaf flush (dry season=February through May).

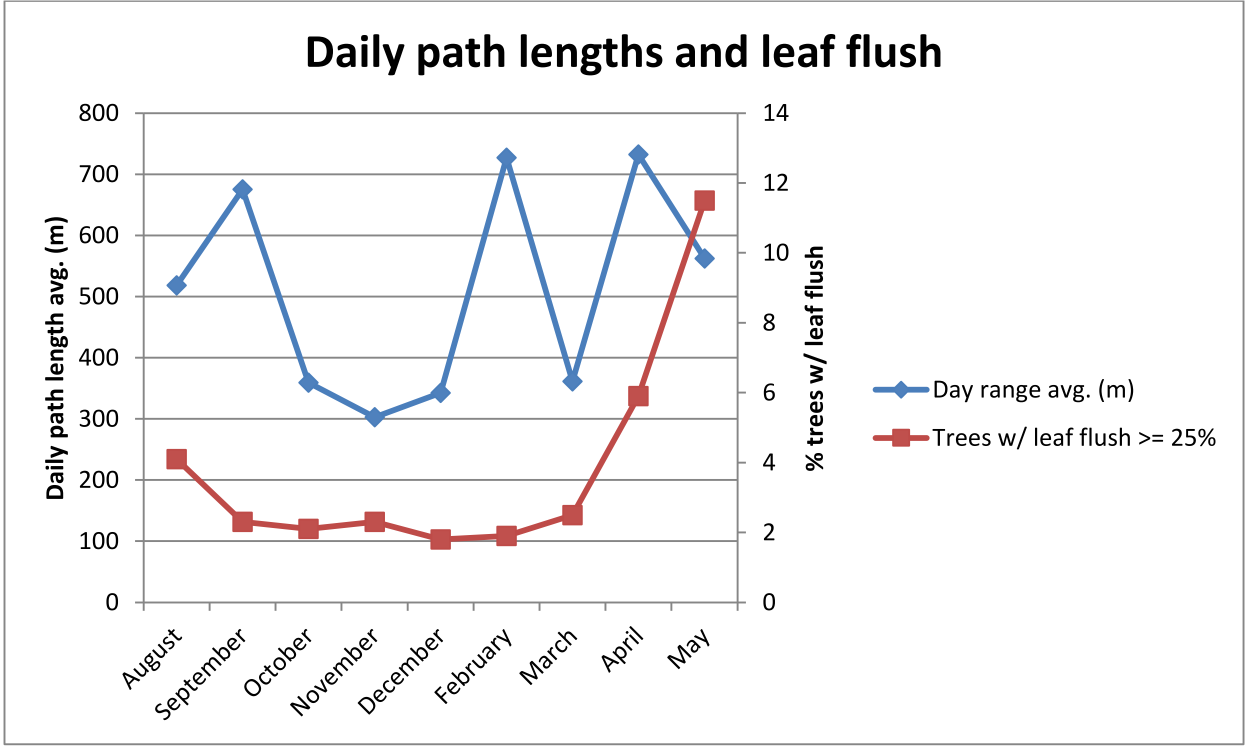


Figure 5.31. Daily path lengths and flowering (dry season=February through May).

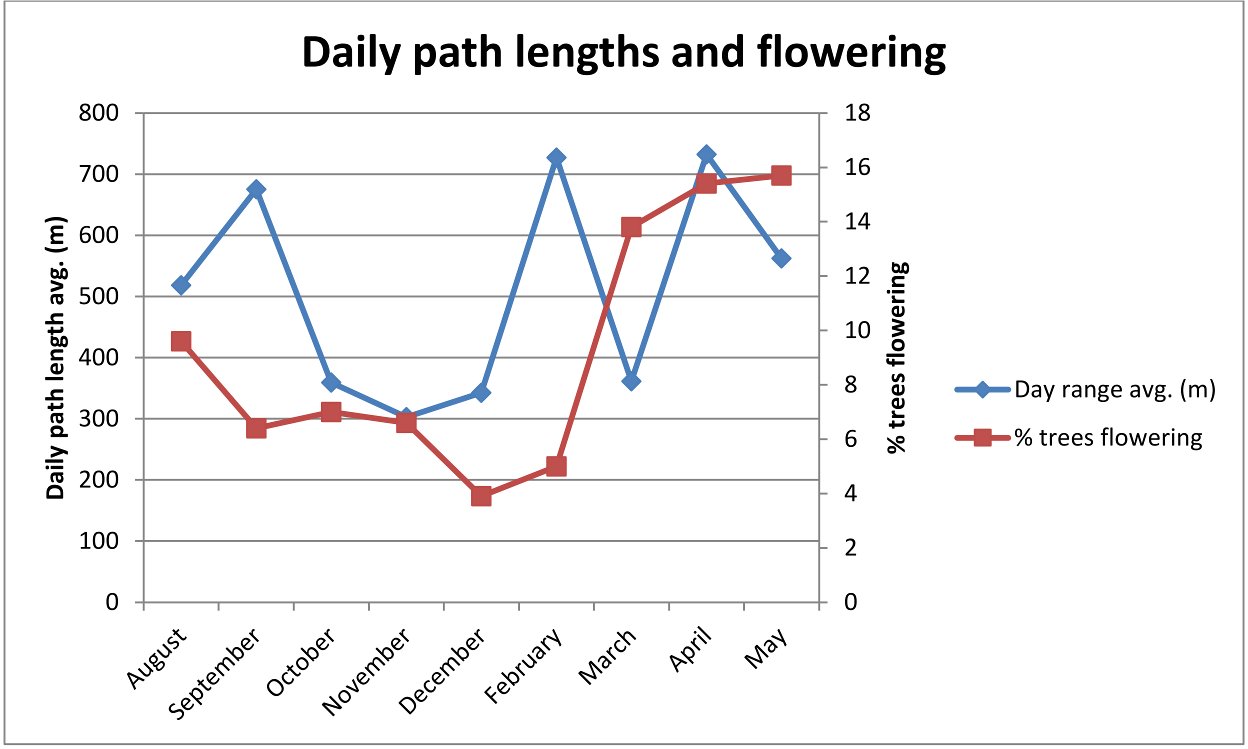


Figure 5.32. Daily path lengths and fruiting (dry season=February through May).

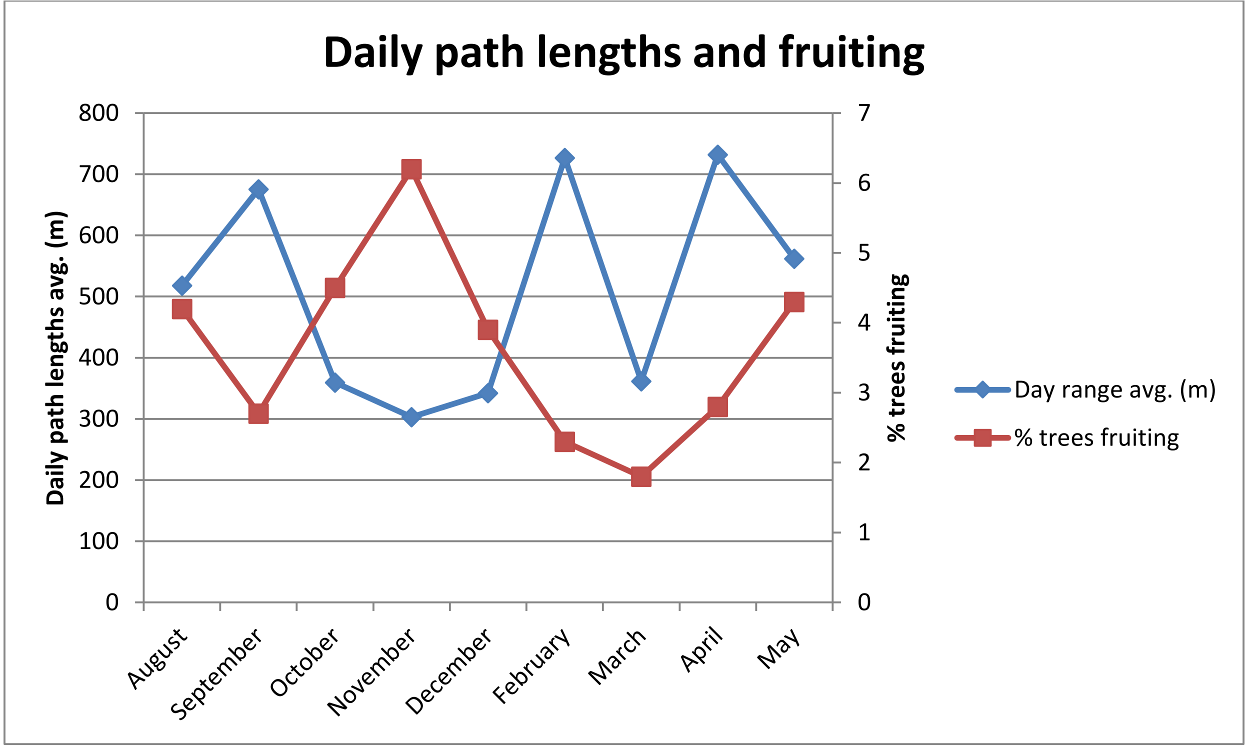
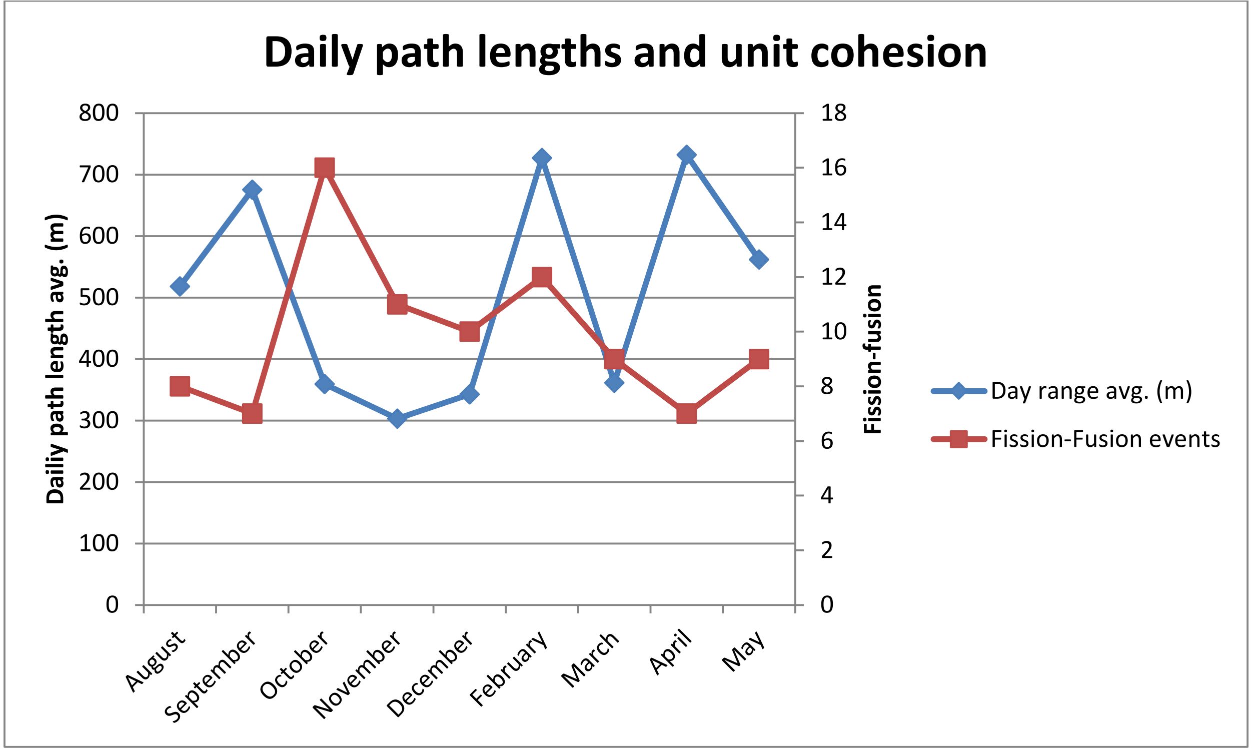


Figure 5.33. Daily path lengths and degree of unit cohesion (fission-fusion).



5.3.4. Additional aspects of organization and structure

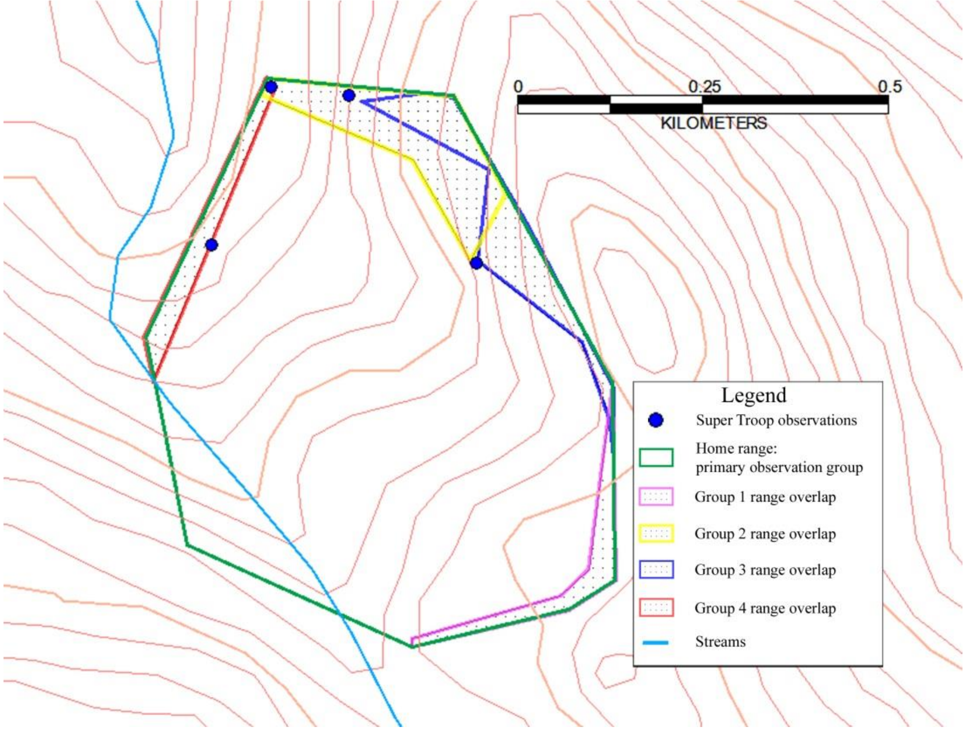
5.3.4.1. Super-trooping

Super-trooping was observed four times during the study, but two of these were with the same super-troop so were only noted as one super-trooping event: three times during June 2010 and once during September 2010, both wet season months. These are shown in Figure 5.34. The observations in June were of two separate super-trooping events. The first of these events was observed twice. It was encountered fusing on June 16th and again in the same area on June 18th during fission. This troop could not be successfully followed on the 16th and the area was not accessed on the 17th of June. Therefore it cannot be confirmed if the groups had remained together for the entire 48 hours between the two observations. This super-troop consisted of at least three groups with an estimated 54 individuals. The two GPS marks along the north-northwest border of the home range of the primary research group in Figure 5.34 are the locations of these observations. The second super-troop observation was on June 30th and appeared to be fissioning during initial encounter. This super-troop consisted of an estimated three groups and a minimum of 44 individuals. The GPS mark along the northeast of the home range periphery is the location of this observation. The last super-troop observation was in September 2010 and comprised an estimated minimum of 44 individuals in at least two groups and occurred during troop fusion. The GPS mark along the western border of the home range of the primary research group is the location of this observation.

All of these super-troop observations involved the primary research group. Super-trooping only occurred during the first half of the wet season (June through September) and may be partially related to temperature which is high during this time. Super-trooping partly overlaps primary or secondary peaks in fruiting and leaf flush, and does not overlap peaks in flowering, so it is not likely to be correlated to phenology.

Super-trooping occurs when home range use is greatest (Figure 5.19) suggesting that increases in ranging variation could be related to the timing of super-trooping. Some behaviors observed during these events are discussed later in this chapter.

Figure 5.34. Location of super-troop observations.



5.3.4.2. Bachelor individuals

All bachelor individuals observed were male; no bachelor females were encountered. There were 13 bachelor individual encounters, including 10 adults and three subadults. Bachelor individuals were not observed in all months. There were four encounters in the dry season and nine in the wet season, which contains twice as many months.

Bachelor individuals were observed within the home range of the primary and secondary research groups. In the home range of the primary research group a bachelor and elderly male was encountered on the periphery of the home range. He avoided being directly observed and traveled along the periphery of the home range moving very quietly. When he approached to within 100 m of one unit of the primary research group, one adult male from the primary group began to alarm call and was joined by other unit members and then by members from a second unit approximately 50 m away. The second encounter with a bachelor male in the primary research group's home range involved a younger male which appeared to be shadowing the group. He followed the group at a distance of about 100 to 150 m. His presence was apparently not detected by the primary research group, but he was startled by my presence, retreated towards the periphery and was not further observed.

In the home range of the secondary research group bachelor adult males were observed twice. The first observation involved an adult male whom remained along the periphery of the group's home range and at a distance from the group of 100 to 150 m. This individual was observed for about two hours, during which he remained at a similar distance from the group as they moved. This individual remained silent and his presence was either not noticed by the group or not acknowledged. The second observation involved a bachelor male and the apparently emigrating subadult of the secondary research group. The group had fed between 14:00 and 15:00 and then moved northeast possibly towards a resting site. At that time the bachelor male appeared, having been about 80 m away from the group to the southwest. He moved to the area where the group had been feeding, and as he did the subadult male appeared from the north and moved to this area as well. They were observed to feed from the same tree less than a meter away from each other. The bachelor male moved on first followed by the subadult, possibly shadowing the secondary research group.

Although not recorded as a bachelor male, the trapped unit of the tertiary research group included an elderly male who maintained a distance of 50 to 100 m between himself and the rest of the unit. This was nearly the maximum possible distance he could maintain given the size and shape of the area they were trapped in.

The observations noted above indicate bachelor males usually remain along the periphery of the home range or at a distance of around 100 m from the group, and when approaching a resident group to within 100 m the group either moves away or alarm calls.

One additional observation involving Group 2 in Figure 5.27 provides data concerning an encounter between a unit and a subadult individual. The subadult and the unit male were an estimated 30 m apart from each other when encountered. The adult male alarm called and the subadult responded with a similarly phrased call an octave higher than the adult male's call, which had frantic and shaky (vibrato) quality. Based on the sound of the vocalizations, the subadult appeared to be a male and was non-aggressive, whereas the adult male was aggressive. After 10 to 15 min of continuous calling back and forth I attempted to move close enough to see the subadult, and in response all doucs fled with the adult male with the unit, and the subadult, in opposite directions.

Based on my observations, bachelor male encounters follow three patterns. The first involves encounters with elderly males, possibly previous resident males of a nearby group, who remain along home range peripheries and do not appear to actively seek residence. The second involves encounters with adult males which appear to shadow the resident group, possibly seeking residence or mates or both. The third involves encounters of subadults, possibly in the process of dispersal. Many bachelor male encounters were not long enough for me to determine into which category, if any, they belonged.

5.3.4.3. All-male groups

Two all-male groups were encountered, the first in April 2010 and the second in July 2010. The first encounter involved three individuals including two adults and one subadult which were traveling and foraging together with a troop of macaques. The second encounter involved at least six individuals including three adults and three subadults. Both encounters occurred in the same area about 200 m apart, but it is unknown if the same individuals were involved. I cannot draw many conclusions from these two observations. What can be noted is that all-male groups occur, but were less frequently encountered than bachelor males. If my two encounters are representative of all-male banding behavior, this implies that the end of the dry season and beginning of the wet season is characterized by increased fusion among bachelor individuals, similar to the increased fusion between units and groups.

5.3.4.4. Immigration and emigration

One observation relating to immigration and one to emigration were made. In March 2011, a subadult female immigrated into one of the units of the primary research group. This individual had not been observed prior to this and she was already part of the unit when first observed, so it is unclear when exactly she immigrated. This event is notable as I never observed bachelor females. It is also possible that she represents one of the confiscated doucs that were released into Son Tra during research. In January 2011, a possible emigration event was observed among the secondary research group when a subadult male of the group begun to travel with a bachelor male, and he remained at a distance of about 100 m from his birth group.

5.3.4.5. Birthing and mating

Infants were observed in almost every encountered unit, however only the six infants of the primary research group are discussed here because their age and consequently the time of their birth can be estimated more accurately.

At the beginning of August 2010, two infants of approximately six months of age were observed in the largest and mid-sized unit of the primary research group. These two infants would have been born around February 2010. At the same time, the smallest unit of the primary research group contained an infant which was between 15 to 18 months old which would have been born between February and May 2009. A forth infant was born into the largest unit of the primary group and was first observed at about one week of age in early March 2011. These four infants suggest a birthing sometime between February and May. The other two infants of the largest unit were estimated to be one year of age at the beginning August 2010, suggesting they were born in August of 2009. Given a gestation period of 180 to 210 days (Brockman & Lippold, 1975; Lippold, 1981), the births that occurred around February through May suggest mating between July through November, and the births that occurred around August suggest mating around January and February. Based on these observations I can only conclude that birthing and mating occur throughout the year (*i.e.*, both seasons).

5.3.4.6. Interspecific associations

Rhesus macaques (*Macaca mulatta*) and doucs were observed to travel or feed together 42 times (28 times during in the wet season, 14 times during the dry season). Common muntjac (*Muntiacus muntjak*) and doucs were observed seven times together (five times during the wet season, twice during the dry season). Associations did not occur in all months and were not evenly distributed across months. Figure 5.35 illustrates the number of observed associations, revealing peaks in associations between August and October.

In 29 of the 42 associations between doucs and rhesus macaques, the primates were associated upon encounter, and in the remaining 13 cases the macaques passed through a douc group. Often the macaques fled in response to my presence shortly after being encountered, but in 15 of the 42 associations there was no apparent interruption due to my presence. The average length of associations was 34.8 min, but the longest association lasted for 8 hours and 44 min. If all associations lasting less than a minute are removed along with the longest association, the average duration is 31 min. Given the short average duration of associations, this suggests associations are opportunistic and do not represent stable mixed troops. In 13 cases the macaques were either with the doucs in the morning before the doucs began activity, or in the late afternoon when douc activity was ending, and apparently had slept near the doucs. Associations might provide anti-predator or protection benefits which may be beneficial around sleeping sites.

In five associations, the macaques were feeding and traveling directly beneath the doucs, which remained above 15 m. However, in all other associations the primates traveled and fed together without a separation in height, suggesting associations increase forging competition.

Douc and macaque monthly associations are compared to temperature (Figure 5.36), precipitation (Figure 5.37), leaf flush (Figure 5.38), fruiting (Figure 5.39) and flowering (Figure 5.40). No correlations were significant. However, Figures 5.40 and 5.41 illustrate douc and macaque associations peak during the secondary peak in fruiting and flowering and just before the primary fruiting peak. It is possible that abundance of high quality foods permits more frequent associations.

Seven douc and muntjac associations were recorded of which six involved a single muntjac individual. Associations lasted between a few seconds to 13 min. In three cases a muntjac was grazing directly underneath the doucs. The remaining four associations were interrupted by my presence and it is unknown if these muntjacs were foraging or merely passing underneath the doucs. During one case a muntjac followed underneath a douc group for 10 min while foraging, and I believe the muntjac was feeding on *Lithocarpus thomsonii* seeds dropped by the doucs. During another case it was confirmed a muntjac was feeding on *Lithocarpus fenestratus* seeds dropped by the doucs during feeding.

Figures 5.36 through 5.40 show the number of associations between doucs and muntjacs on a monthly scale in relation to weather and phenology data. No correlations were significant. This association is not stable, but appears to provide a foraging benefit for the muntjacs which feed on otherwise inaccessible seeds dropped by the feeding doucs.

Figure 5.35. Number of interspecific associations (dry season=February through May).

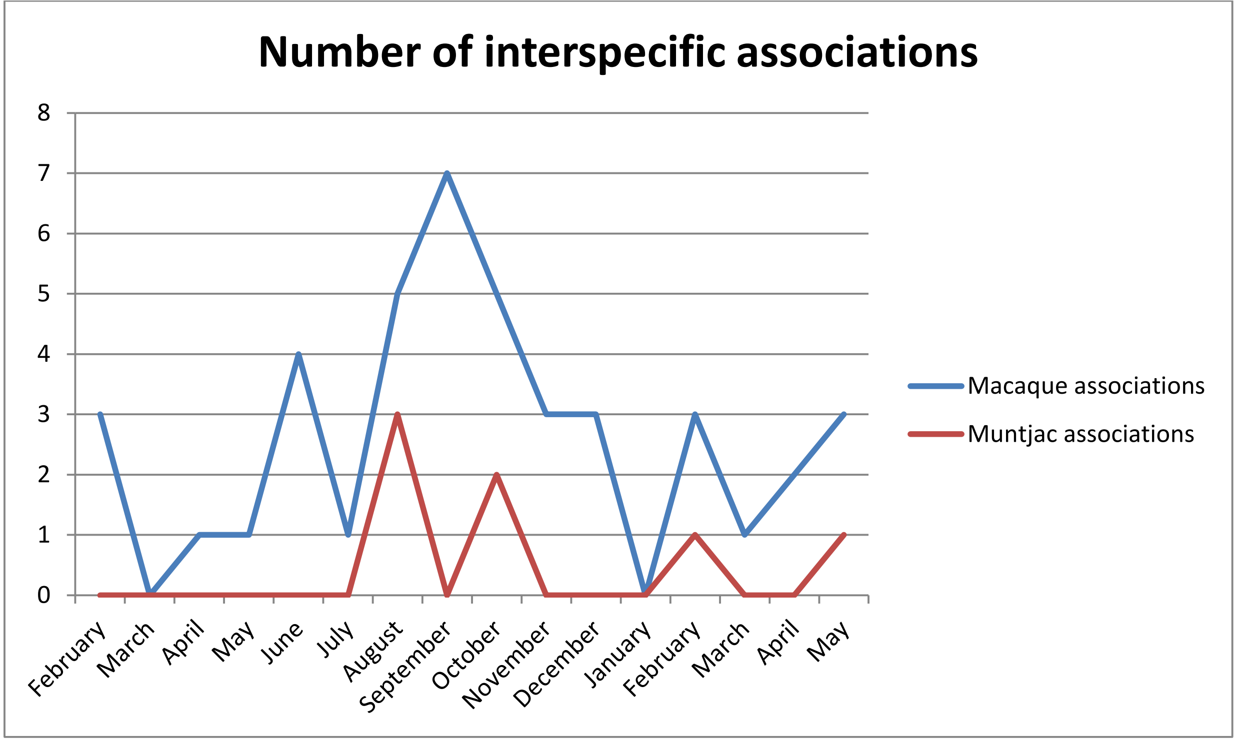


Figure 5.36. Interspecific associations and temperature (dry season=February through May).

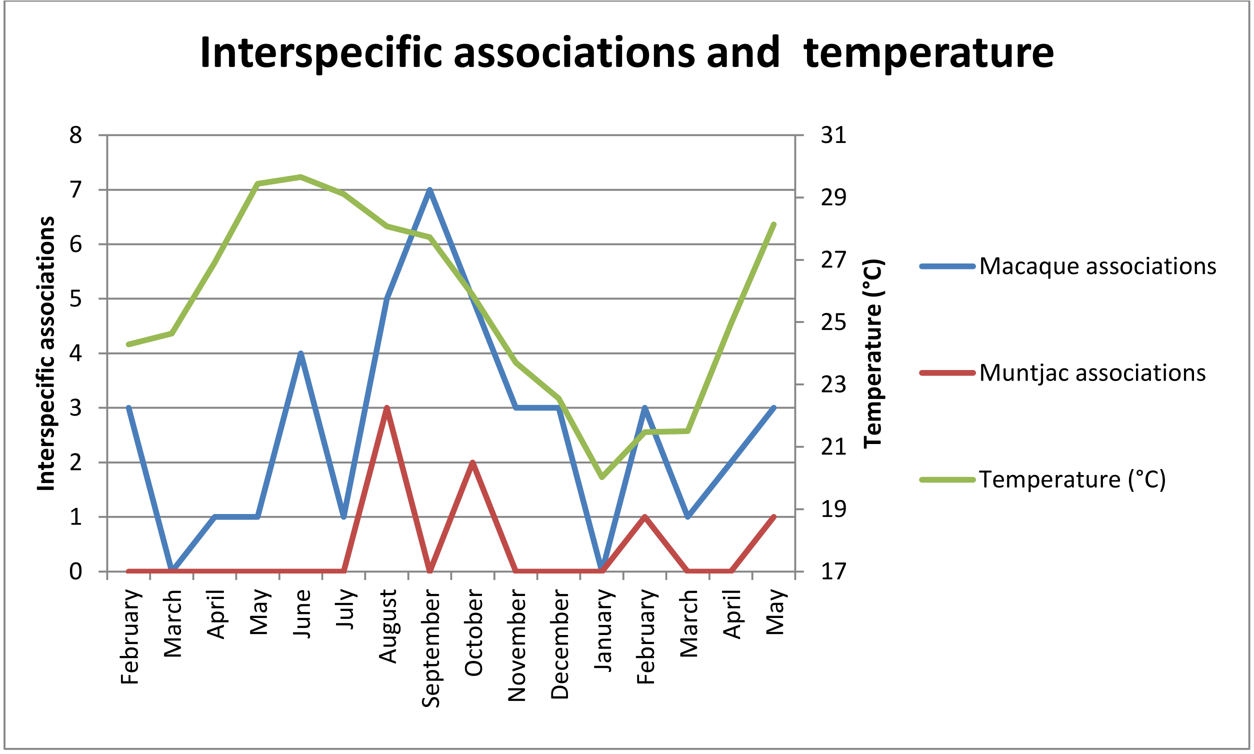


Figure 5.37. Interspecific associations and precipitation (dry season=February through May).

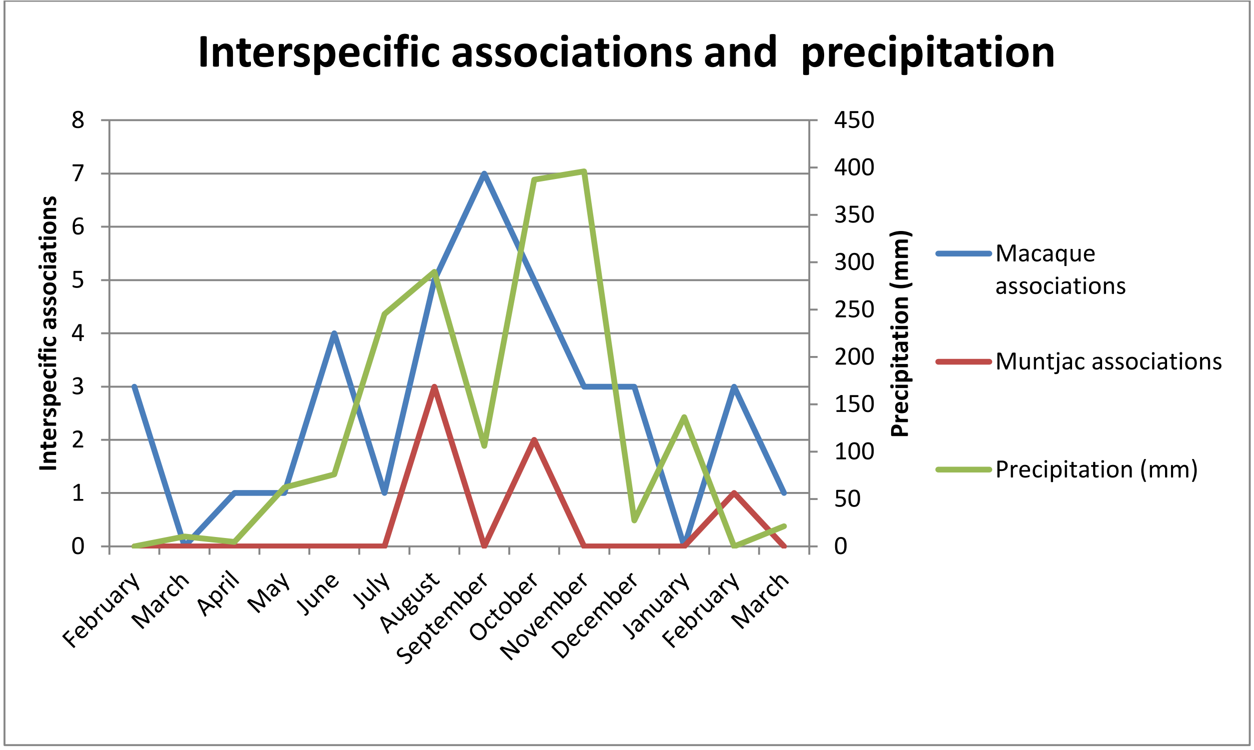


Figure 5.38. Interspecific associations and leaf flush (dry season=February through May).

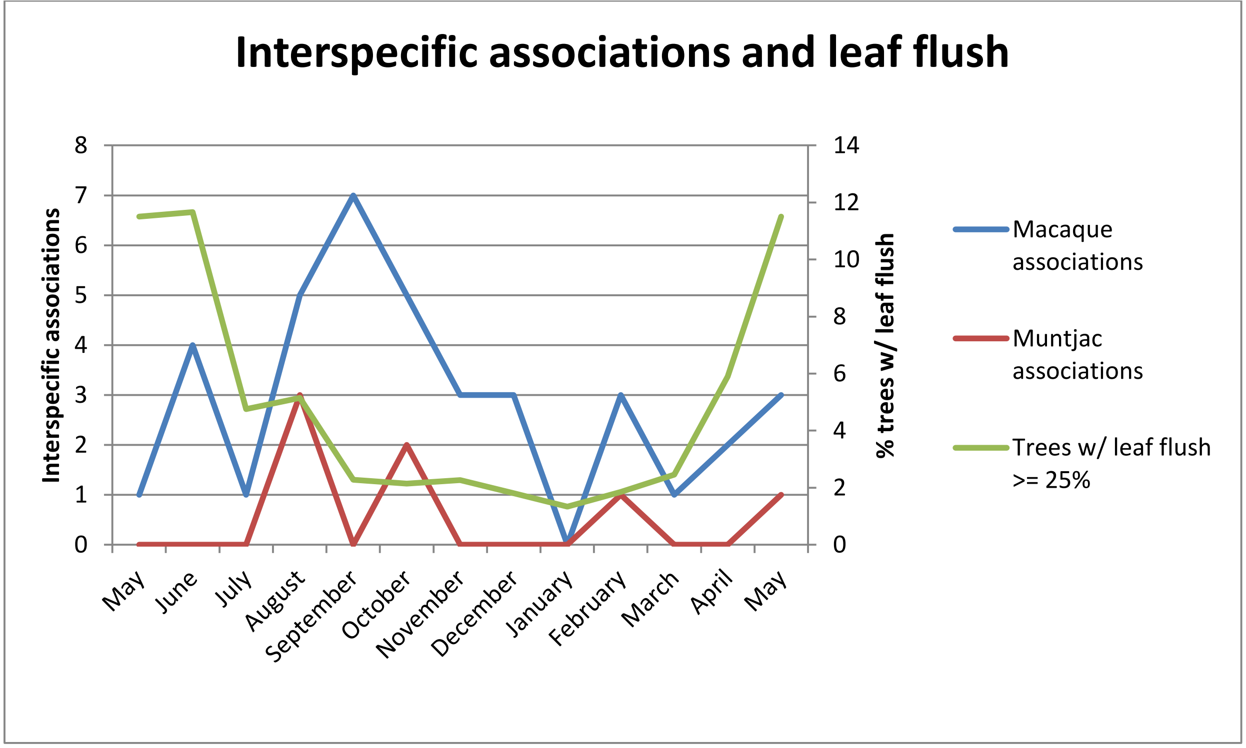


Figure 5.39. Interspecific associations and fruiting (dry season=February through May).

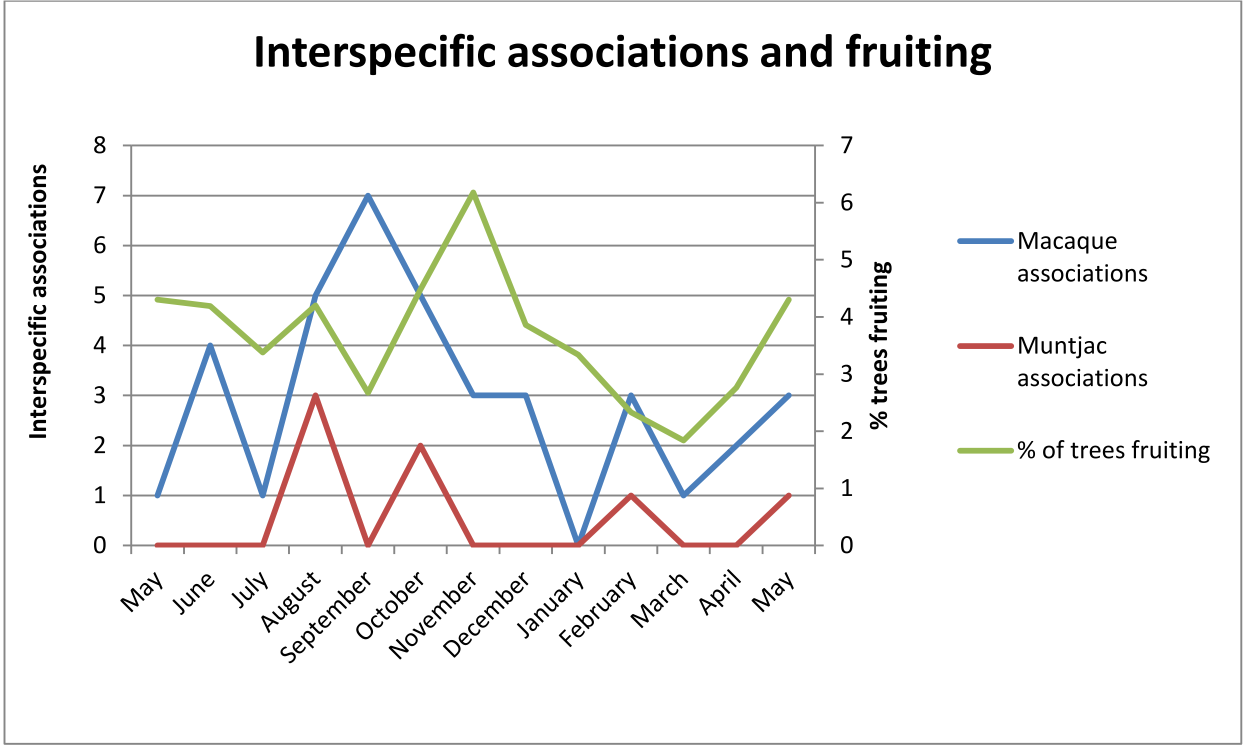
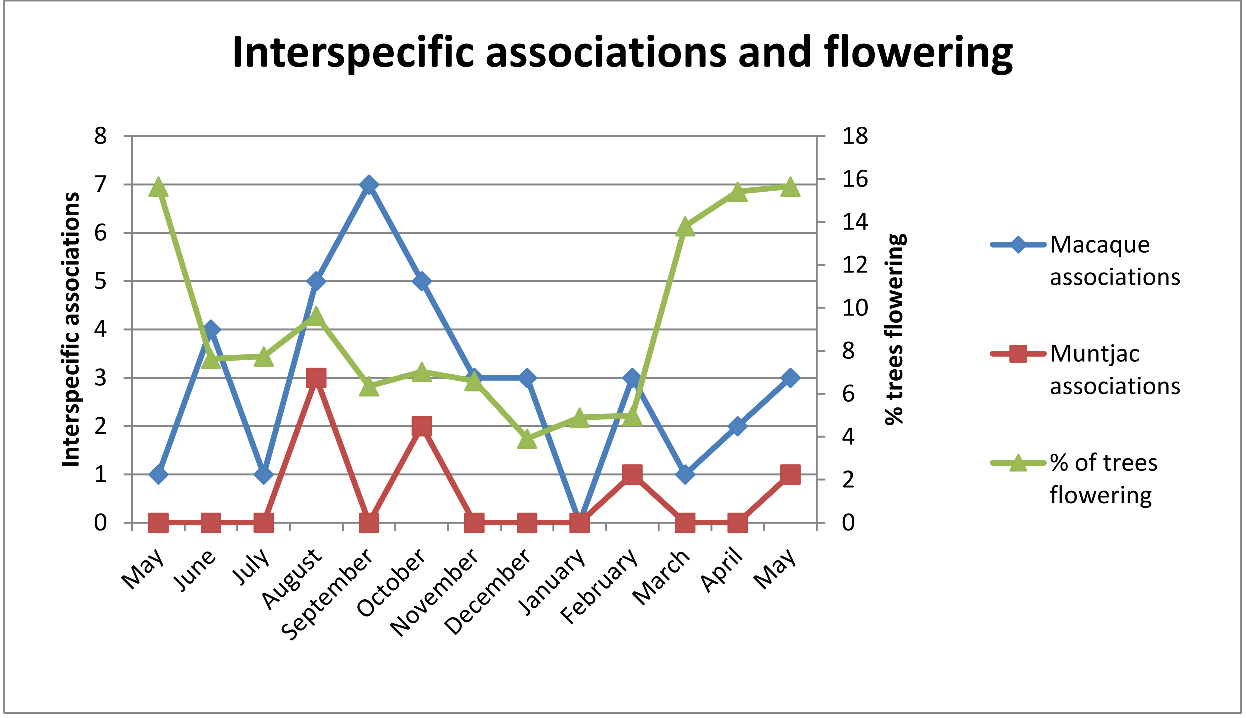


Figure 5.40. Interspecific associations and flowering (dry season=February through May).



5.4. Discussion

5.4.1. Unit and group size on Son Tra

The average unit size is 6.5 ± 1.2 individuals. The average group size is 18.0 ± 3.6 individuals, and groups consist of an average of 2.7 ± 0.6 units. Both unit and group sizes are comparable to other *Pygathrix* and colobine studies.

For red-shanked doucs, Lippold (1977) reported an average of nine individuals per group although she does not distinguish between groups and units. Pham Nhat (1993b) reported groups of red-shanked douc range between 4 and 27 individuals, which clearly represents both units and groups. Lippold (1998) reported a 51 individual group which is possibly a super-troop and is comparable to super-troop sizes found in my study. The average group size observed in my study is slightly larger than previous studies at Son Tra which reported an average group size of 14.3 individuals (Lippold & Vu Ngoc Thanh, 2008) and 15.2 individuals (Dinh Thi Phuong Anh et al., 2010). Phiapalath et al. (2011) reported group sizes of two groups in Hin Namno Protected Area in Laos at an average of 24.5 individuals. One of these groups contained between 17 and 20 individuals and probably reflects a single group. The other group contained between 25 and 40 individuals. If both groups counted by Phiapalath represent single groups, this indicates groups on Son Tra are comparably small. However, in Phiapalath's second group the high end of his estimate is nearly double the low end, and the group was only observed to be this large during part of his study, suggesting super-trooping.

Ha Thanh Long (2009) reported groups of grey-shanked doucs in Kon Ka Kinh National Park, Vietnam to comprise 14.8 individuals. His observations range from two to 88 individuals which suggests that units, groups and super-troops are included in the analysis although these are not distinguished. Nearly 75% of groups encountered in Ha Thang Long's study were smaller than the average group size he had calculated, suggesting the reported average group size overestimates unit size and underestimates group size. Overall group size in my study is slightly larger than group size reported in Ha Thang Long (2009).

Rawson (2009) reported units/groups of black-shanked doucs in Seima Biodiversity Conservation Area, Cambodia to comprise 7.52 ± 5.22 individuals. This number is slightly higher than unit sizes reported in my study, but his analysis includes groups of 26 individuals and obviously includes both group and unit levels of social organization. Although Rawson's (2009) analysis inflates unit size, it is best considered as a unit level analysis. Ngo Van Tri (2003a; 2003b) reported unit sizes of black-shanked doucs in Yok Don National Park, Vietnam at 5.16 ± 1.5 individuals in the wet season and 6.44 ± 4.33 individuals in the dry season. His analysis is clearly at unit scale, and is slightly lower compared to unit size reported in this study. Hoang Minh Duc (2007) reported 8.8 ± 3.0 individuals in Nui Chua National Park, Vietnam, and 7.7 ± 3.2 individuals in Phuoc Binh National Park, Vietnam, at unit scale and only among one-male units. Although his reported unit size and the unit size in my study are comparable, his analysis included only one-male units, not multi-male units. Therefore his analysis underestimates unit sizes. Hoang Minh Duc (2007) also reported averages for multi-male units which he considered together with groups. Based on the number of individuals per group in his analysis (13 to 45) it appears he may have included multi-male units, groups, and super-troops in the group level analysis. However, Hoang Minh Duc (2007) is the first *Pygathrix* researcher to consequently distinguish between unit and group levels of social organization. Group sizes were reported at 22.8 ± 9.0 individuals in Nui Chua National Park and 12.8 ± 1.3 individuals in Phuoc Binh National Park. Group size reported in my study is comparable despite his inclusion of multi-male units and super-troops.

The average group size in this dissertation is within the upper range of group sizes reported for Asian colobines (see Table 2.9). Unit sizes calculated in my study also fall in range of Asian colobine group size, but along the lower end. It seems group sizes of Asian colobines as reviewed in Chapter 2 may reflect unit scale among some primates, although not all Asian colobines have a comparable modular social organization as described here for the doucs and has been described for other snub-nosed monkeys. Unit and group sizes on Son Tra are not different from other *Pygathrix* and Asian colobine studies, suggesting Son Tra is a comparable research site and data is representative.

5.4.2. Ecological constraints

One explanation for unit and group size is the ecological constraints model (Chapman et al., 1995; Gillespie & Chapman, 2001; Terborgh & Jansen, 1986; Wrangham et al., 1993). This model suggests that feeding competition within a group limits group size, and therefore food availability and environmental factors which influence food availability affect group size. Some studies caution against the use of this model for explaining group size among folivorous primates (Chapman & Pavelka, 2005; Struhsaker & Leland, 1987; Yeager & Kirkpatrick, 1998). However, the small home range of the primary research group increases competition between units, and potentially minimal home range overlap between groups suggests intergroup competition and possibly territoriality are significant. Therefore aspects of ecological constraints are explored here, including habitat, infanticide, predation and dietary influences.

5.4.2.1. Habitat

Habitat availability, quality and disturbance possibly have an effect on group size. Habitat disturbance on Son Tra is moderate (see Chapter 3), although doucs were regularly encountered along all transects regardless of the degree of disturbance. Habitat disturbance does not predict group size or density. Fedigan & Jack (2001) illustrated that if regenerating forests are protected, they are utilized by primates. Heiduck (2002) reported food species density was a greater indicator of habitat use than disturbance. Rylands et al. (1993) and Strier et al. (2000) noted that some primates even thrive in disturbed habitats.

Fedigan & Jack (2001) reported the folivorous *Alouatta palliata* expanded into regenerating forests through the creation of new groups rather than changes in group size, as opposed to other and more frugivorous primates in the same area. If this relationship is transferable to the primates on Son Tra, it implies that density of the folivorous doucs rather than unit or group size reflects the influence of ecological constraints.

Density of *Alouatta* species have been found to be influenced by habitat quality (Peres, 1997) and anthropogenic pressure (Cullen et al., 2001; Martins, 2005; Pinto et al., 2009). Pinto et al. (2009) further reported that density decreased with decreasing size of habitat fragments. Bicca-Marques (2003) illustrated greater fragmentation resulted in smaller home ranges. A similar pattern has also been described for *Colobus angolensis* (Anderson et al., 2007). The high density of doucs on Son Tra indicates that high densities of this species can be found in small areas. Forests on Son Tra are becoming fragmented by road construction and development, but the reported home range size of the primary research group is similar to home range sizes reported by Hoang Minh Duc (2007) and Rawson (2009) which studied in sites of much larger areas and with minimal fragmentation. Although habitat pressure likely influence wildlife on Son Tra it is unclear to what degree they affect unit and group sizes or density of the doucs.

5.4.2.2. Infanticide risk

Infanticide has been observed among colobines including *Colobus guereza* (Harris & Monfort, 2003; Onderdonk, 2000), *Colobus vellerosus* (Sicotte et al., 2007; Teichroeb et al., 2009), *Procolobus badius* (Struhsaker & Leland, 1985), *Semnopithecus entellus* (Hrdy, 1974; Newton, 1986; Newton, 1992; van Schaik, 2000), and *Trachypithecus leucocephalus* (Lijie Yin et al., 2012; Qing Zhao et al., 2011) (see also Hrdy, 1979 for a review). However infanticide itself is rarely observed and is usually inferred.

Treves & Chapman (1996) illustrated that among *Presbytis* species group sizes increased when all-male bands were more abundant to reduce the risk of attacks, take-overs and infanticide. Crockett & Janson (2000) predicted that an increase in the number of adult females in a group initially correlates with increases in infanticide. Teichroeb et al. (2012) reported among *Colobus vellerosus* that multi-male groups have increased infanticide risk compared to one-male groups because they attract more immigrating males. In this study I observed an increase in all-male groups during the same time when units are generally more cohesive and when super-trooping occurs. In relation to infanticide studies, this suggests an increase in infanticide risk. Yet, there was a striking near absence of physical and vocal aggression observed between doucs during this research, and certainly no observation of a take-over or infanticide. Grunau & Kuester (2001) suggested that because folivorous colobines rely on a more dispersed, low quality food resource than frugivores, and more classic socioecology models predict that their social relationships are more egalitarian than the complex hierarchical social systems of frugivorous primates. To date no infanticide has been reported in doucs, both in the field and captivity, and this suggests infanticide risk does not significantly influence douc behavior.

5.4.2.3. Predation risk

Predation risk has been shown to influence group sizes among primates (Isbell, 1994; van Schaik, 1983). Several studies have illustrated that the large social groups of *Procolobus tephrosceles* and the interspecific associations they form are a function of predation risk from chimpanzees (Boesch, 1994; Busse, 1977; Stanford, 1995). This predator-prey system has not been reported among Asian colobines, although there are observations of behavioral responses to potential predators such as adult males distracting a predation risk from females and infants (Struhsaker & Gartlan, 1970; Tilson & Tenaza, 1976). Tilson (1977) suggested the high frequency of monogamous social organization in *Presbytis potenziani* and *Simias concolor* were a result of a lack of predators. No predation has been observed on *Pygathrix* anywhere, but felids, reptiles, and birds of prey which are known to predate on primates are found on Son Tra (see appendices)

Van Schaik & van Noordwijk (1989) and van Schaik & Horstermann (1994) illustrated that predation risk leads to greater male representation within a group, and males in these groups tend to be more vigilant, more frequently detect, deter and distract predators. In the latter study they compared groups of similar sizes of folivores across continents, including Platyrrhini (*Alouatta* species), African colobines (*Colobus* species) and Asian colobines (*Presbytis* species). They found that Asian colobines have significantly fewer adult males per group, indicating that predation risk is low. However, Yeager (1992) suggested the fusion of units among Asian colobines might be a function of predation pressures, and can occur without the necessity for multi-male units. The strong bond between units observed among doucs in this study suggests male bonding strategies as would be expected in modular societies, but the influence of predation risk on douc social systems cannot be determined at present.

5.4.2.4. Dietary influences and scramble competition

Milton (1979; 1980; 1981; 1998) developed a protein-to-fiber model suggesting the ratio of protein-to-fiber in mature leaves predicts population size. Fimbel et al. (2001) provided support for this model illustrating that the quality of mature leaves in Nyungwe Forest Reserve, Rwanda, permits *Colobus angolensis* to form super-troops of up to 300 individuals, compared to habitats where the mature leaves are low in protein and conspecifics only form groups between two and 20 individuals. In this study I report that dietary quality likely influences group sizes and feeding budgets on Son Tra (see Chapter 6 and Chapter 7).

Wrangham et al. (1993) and Chapman & Chapman (2000a) found that food competition limits group size because larger groups will deplete food resources faster, increasing the degree of scramble competition and necessitating increased travel. More energy is required in larger groups in order to meet the daily nutritional requirements of each individual. Conversely, leaves are widely distributed and consistently available compared to higher quality food resources. Colobines exploit mature leaves and possess the physiological adaptations to maximize nutritional extraction from mature leaves. Several studies suggest food competition among folivorous primates does not limit group size (Isbell, 1991; van Schaik, 1989; Yeager & Kirkpatrick, 1998). In this study I did not find a relationship between ranging and food availability, food availability and the frequency of fission-fusion events, or ranging patterns and the frequency of fission-fusion events. Because young leaves and fruit are available throughout the year on Son Tra, food competition would appear to be low, and therefore larger groups would appear to be nutritionally permissible and beneficial given the reduction in predation risk and absence of infanticide risk. However, the group size of doucs is small, and group sizes are generally small among folivorous primates. The lack of larger groups is unexplained and is termed the “folivore paradox” (Koenig & Borries, 2002; Steenbeck & van Schaik, 2001). Fission and fusion frequency rather than group size may be a more appropriate measure for food competition among doucs, and in Chapter 6 daily fission-fusion patterns are shown to be an adaptation to scramble competition.

As reported, red-shanked douc units are cohesive with daily fusion in the evenings and often around mid-day, regardless of weather and phenology variables. However, the degree of fission-fusion fluctuates and is significantly correlated with leaf flush; units spend the greatest amount of time in a fused state when young leaves are most available. This supports the scramble competition hypothesis, indicating higher quality food availability permits increased fusion because less energy is needed to meet daily nutritional requirements.

5.4.3. Unit structure and plasticity

Chapman & Rothman (2009) illustrated that social structure and composition within a single population can be diverse. In this study, the primary research group contained three units which had a different social structure; one was monogamous, one was a one-male unit, and the last was a multi-male unit. If ecological conditions were a determining factor in unit social structure, they had minimal influence considering all units share the same home range. If predation pressures were influential then units would be larger, although regular fission-fusion of units does reduce predation risk. The influence of infanticide is likely absent as no infanticide was ever reported among doucs.

Results from this study support the classic socioecology models, suggesting intragroup scramble competition may be a factor acting to reduce unit and/or group sizes, and the pattern of fission-fusion, in combination with potential ecological constraints and nutritional influences.

Finally, Grueter & van Schaik (2010) hypothesized that the one-male unit among colobines is an ancestral social system, with modularity representing a derived state. Forces that influenced the ancestral formation of the one-male unit have been reduced, and the newly evolving social structures are being molded under varying forces to varying degrees. Chapman & Rothman (2009) referred to this as phylogenetic inertia and noted it was a major influence in social system plasticity. If any single or combination of variables tends to select for a specific social system or structure, they have clearly become relaxed given the degree of structure diversity observed in my study. Phylogenetic inertia offers one explanation for this diversity.

5.4.4. Social organization – modular societies

Our understanding of modularity and fission-fusion among primates is still evolving (Aureli et al., 2008). Fission-fusion can no longer refer to a singular type of social system, but a continuum of degrees and characteristics. Modular and fission-fusion based societies are different, although modular societies do involve fission and fusion behavior. In modular societies, the membership of different scales of social organization (e.g. units and groups) is not flexible, whereas in fission-fusion societies membership can be flexible. Modularity has been suggested for only a few primate species, including the *Rhinopithecus* species, *Nasalis*, *Papio hamadryas*, and *Homo sapiens* (Bennett & Sebastian, 1998; Grueter & van Schaik, 2009; Grueter & van Schaik, 2010). My study supports modularity in *Pygathrix*, especially as unit membership is not flexible, groups are composed of multiple units and membership is not flexible, and the home range of a group is not divided among units but shared and perhaps defended. As explained previously, fission and fusion behaviors have been observed among all *Pygathrix* species, although only Hoang Minh Duc (2007) distinguished units from groups. In this study there was a daily pattern of fission and fusion between units. However, there was no fluidity in unit size, structure or membership.

Modularity and the fission-fusion behavior of doucs differs from other primates living in a fission-fusion society with flexible unit membership, which is also referred to as individual-based fission-fusion societies and occurs in *Ateles* species (Chapman, 1990; Wallace, 2008), *Pan* (Lehmann & Boesch, 2004), some *Papio* species (Grueter & van Schaik, 2010), and possibly

Pongo (van Schaik, 1999). The modular society of doucs does resemble group-based fission-fusion societies aside from the flexibility of unit membership, which occurs in *Cacajao* species (Bowler & Bodmer, 2009; Garber & Kowalewski, 2013; Heymann, 1992) and *Macaca fascicularis* (van Schaik & van Noordwijk, 1986; van Schaik & van Noordwijk, 1989). As noted by van Schaik & van Noordwijk (1989), *M. fascicularis* groups fissioned into units referred to as foraging parties when fruit was scarce. My observations showed a similar pattern as groups tended to fissure into units when young leaves were scarce. Although fission-fusion in doucs provides social benefits, the ecological determinates like leaf flush and precipitation provide quantified explanations for this behavior.

The pattern of fission and fusion among doucs may also regulate feeding competition, a concept described by Kummer (1968). Ramos-Fernandez et al. (2006) created a computer based foraging model, and reported that societies which incorporate fission and fusion can form based on resource patch distribution and size. In their models, if resources were not overly scarce resulting in increased competition, or overly abundant resulting in decreased competition, fission and fusion could manifest naturally, leading to bond formations and complex social networks such as those within modular societies. Lehmann et al. (2007) developed a similar foraging model for *Pan*, which accurately predicted location and group size of current populations of *Pan*, and suggested that travel costs are a limiting factor which can be reduced by fission into foraging units. The pattern of fission and fusion among the doucs on Son Tra does appear to regulate feeding competition (Chapter 6).

Calls between the males of the various units within a douc group appear to initiate fusion. Ramos-Fernandez (2005) recorded that in *Ateles geoffroyi*, males respond to playbacks of loud calls from a familiar resident male by approaching, but they do not approach the call of an unfamiliar non-resident male. During my study, males of different units of the primary research group almost always called in response to another resident male's loud call. When a threat was detected, loud calls initiated fusion as the calling male's unit moved toward the responding male's unit, while the adult male(s) that initiated the call remained behind until all members had moved away from the threat. However, when bachelor males or a non-resident unit were near, the responding male and his unit moved towards the calling male's unit. This suggests strong unit bonds and male/female alliances within a group as well as distinction in calls which provide a coordinated group-level behavioral response.

Concerning the one-male unit, van Schaik & van Hooff (1983) noted multi-male units arise when one-male units cannot monopolize access to breeding females. One-male units typical of Asian colobines can be found alongside multi-male units in doucs, possibly suggesting that multi-male units comprise lower quality males unable to monopolize breeding females, or that the costs of intergroup resource defense to a single male outweighs the costs of monopolizing breeding females. Considering the presence of bachelor males and all-male groups with the imminent risk of take-overs, it is possible that regular fission and fusion among units permits for similar alliances aimed at resource defense. Vocalizations as described above serves to support this suggestion. This does not contradict the benefits of the one-male unit, and as long as the units remain static, males in one-male units can still be assumed to monopolize breeding females. Males of one-male units may be of greater quality than other males, and females may preferentially select them for breeding and protection. Multi-male units and groups permit for male alliance and protection of resources. Therefore the one-male unit within a modular society combines the benefits of both structures.

Garber & Kowalewski (2013) reported on the breeding system of *Cacajao* species, which have fission-fusion based social system that resembles modularity. They suggested the breeding system was multi-male, with males tolerant of the sexual activity of other males because of kin relationships and male alliances. In this study, all but one mating observation occurred within when units were fused, suggesting mating is tolerated between males.

There is a division of social organization for the doucs on Son Tra into three non-flexible levels, strongly suggesting modularity. First there is the basic unit, which may be one-male or multi-male, and membership is not flexible. Second there is the group, which is composed of multiple units, is strongly bonded, and membership is not flexible. Last there is super-trooping, which involves multiple groups and is neither regular nor cohesive.

5.4.5. Modular societies and intergroup contest competition

Grueter & van Schaik (2009) illustrated a significant relationship between body mass dimorphism and male contest competition within modular societies in Asian colobines. Modularity increases contest competition over access to mates and is intensified as units are often shadowed by bachelor males and/or all-male groups. Their contemporary socioecology models relating to modularity are applicable to the doucs on Son Tra. Male contest competition may be a driving force behind several patterns observed in my study, for example the absence of intragroup male aggression, bachelor males which shadow groups, the presence of intergroup aggression, what appears to be minimal home range overlap between groups, and the absence of bachelor females. However, in contrast to colobines studied by Grueter & van Schaik (2009) the doucs cannot be considered a "high-intensity" species because aggression (stares, displays, chases, physical contact) was infrequent within groups. Also, there is no known incident of infanticide among *Pygathrix* in any wild or captive study. The doucs can be considered a "high-frequency" species given the many daily male-male encounters. Increases in male contest competition within modular societies should accompany greater sexual dimorphism. Supporting this relationship among doucs is canine dimorphism, which is more pronounced in *Pygathrix* and *Nasalis* amongst all Asian colobines (Plavcan et al., 2005). Additionally, there is body size differences discussed in Chapter 2. Grueter & van Schaik (2010) further explored factors influencing the development of modular societies and found that they are common in Asian colobines where bachelor males or all-male groups pose a threat in potential take-overs or infanticide. A modular society is a social benefit with low ecological cost, particularly as folivory is based on non-limiting resources. Fashing (2001b) reported males may be indirectly defending mates by primarily defending resources. Harris (2006) observed core areas among *C. guereza* were defended more aggressively, and consequently relates behaviors during intergroup encounters to food competition. These studies highlight male contest competition is a driving force in colobine society, and this appears to be a significant force for the douc on Son Tra, which is intensified given the live in a modular society.

Female contest competition can affect female relationships and reproductive success (Harris, 2006; Koenig, 2002). Females were active participates in intergroup aggressive encounters. On one occasion an adult female physical preventing an adult male from displaying towards and following a female from another unit, suggesting intragroup contest competition.

Korstjens et al. (2005) reported female aggression during intergroup encounters may relate to resource defense. Crockett & Janson (2000) predicted females compete in order to minimize group size in areas where foraging costs and ecological constraints affect group sizes, this way they increase their own infants' chance of survival. Females may not compete to limit group size, but instead compete for quality males. This is in agreement with Sicotte & MacIntosh

(2004) who found both male and female *C. vellerosus* are involved in mate and resource defense. For this same species, Teichroeb et al. (2012) speculated that males of one-male units are of higher quality than males of multi-male units, because they display more frequently and dominate more encounters. Multi-male units attract greater male immigration and thus have higher risk of infanticide, and males of one-male units consequently provide greater protection to resident females and their offspring. This is quantified by Harris (2010), who reported that *C. guereza* were more likely to win aggressive encounters if the group had less adult males, a larger adult male, and was smaller in group size. Newton (1988) also speculated on the fitness and dominance of resident males of one-male units, suggesting a male that can successfully monopolize the resident females will maintain the one-male unit organization, otherwise multi-male organization will arise. Female *P. thomasi* have been found to select males that provide the best protection to their offspring, and assess this quality based on age and vocalizations of the male (Steenbeek et al., 1999; Sterck et al., 2005). Sicotte et al. (2007) reported that male calls in *C. vellerosus* announce competitive ability and Delgado (2006) reported adult male loud calls are related to sexual selection.

Comparable incidents of female mate competition and interference in courtship have been reported in *R. roxellana* (Baoguo Li & Dapeng Zhao, 2007). Female mate competition implies that adult males offer a significant benefit to females and their offspring. Adult males were regularly observed to defend the group in my study, and most frequently to protect infants. In all cases in which the group felt threatened, the adult male(s) always protected infants by positioning themselves directly in front of the infant and between the infant and the threat. Similar behavior was noted by Lippold (1977) and Phiapalath (2009).

It is not possible for me to analyze the influence of male and female competition, although male contest competition appears to have a greater influence on douc society.

5.4.5.1. Banding behaviors

Super-trooping, unit cohesion and all-male groups all appear to peak around the same time on Son Tra. The degree of fission-fusion observed in this study indicates the degree of unit cohesion, and units are significantly more cohesive during peaks in leaf flush and significantly less cohesive during peaks in precipitation. Otto (2005) studied douc diets in captivity, and based on her observations suggested fission to be more common during leaf flush scarcity. This pattern is not supported in my study. Results of my study support the scramble competition hypothesis indicating greater young leaf availability permits greater fusion through less competition. This suggests that banding behaviors, whether between units, groups or bachelor males, peaks with availability of young leaves as a high quality food resource. Banding behavior may be therefore independent from social influences.

The allee principle suggests the timing of super-trooping is mate location. Evolution of behaviors which increase density during mating season contribute to population growth (Wells et al., 1998). If mating occurs between groups during super-trooping on Son Tra then this reduces the risk of inbreeding and maximizes genetic diversity. Therefore the occurrence of super-trooping on Son Tra may have mating benefits.

Additionally, Bowler & Bodmer (2009) suggested bonds between bachelor males may be useful in take-over attempts and therefore the formation of all-male groups on Son Tra may be a function of increases in unit and group fusion and part of the males mating strategy.

5.4.5.2. Territoriality

Territoriality as defined by Davies & Houston (1984), Feldhamer et al. (2007) and Wilson (2000) is the exclusion of a defined area and the resources within that area to a single group. There appears to be a minimal amount of overlap in home range between groups because adjacent groups are only near each other when they are along the borders of their home range. This might suggest a degree of territoriality between groups.

Mitani & Rodman (1979) created a formula to predict the degree of territoriality among primates. Their formula compares daily path lengths to home range, and is given as $D = d/\sqrt{(4A/\pi)}$, where D is the defensibility index, d is daily path length in km, and A is home range in km^2. If D is greater than or equal to 1 the primates are predicted to be territorial, and if it is less than one the primates are considered non-territorial. The defensibility index of the primary research group is 752, suggesting doucs on Son Tra are territorial. This assumption has been made in earlier studies of the taxon (Hoang Minh Duc, 2007; Pham Nhat, 1993c).

Chapman (1990) and Wallace (2008) noted that among *Ateles*, which live in a society similar to the modular society in doucs, the males appear to cooperate to defend the home range as a means of mate defense. Wallace (2008) found that *Ateles chamek* units are significantly larger (fusion) when they are closer to the periphery of their home range, and smaller nearer the core. Similar patterns might characterize the doucs on Son Tra.

5.4.6. Home range and daily path lengths

Home ranges of colobines vary, and home range can vary greatly within species and habitats (Chapter 2). Home range size for doucs in this study is comparable to the black shanked doucs in southern Vietnam (Hoang Minh Duc, 2007).

Clutton-Brock & Harvey (1977) noted that folivores tend to have smaller home ranges because leaves are less dispersed than fruits and other high quality food resources. Terborgh (1983) illustrated that home range size is smaller when food resources are more abundant. Bennett & Sebastian (1988) observed that high population density and home range size in colobines are an indicator of food resource abundance. These studies suggest that high quality food resources on Son Tra may be abundant. As shown in Chapter 4, high quality food resource are available throughout the year in low quantities, and in Chapter 7 it is shown that mature foliage is of relatively high quality.

Andre (2011) reported that in the same forest the home range of *C. angolensis palliates* groups in areas of greater disturbance were larger than in areas with intact forest. Dunbar (1987) illustrated that population density of *C. guereza* is inversely correlated to home range size. Therefore, a relatively intact forest with a high density might explain the small home range size in Son Tra.

Most colobines have small daily path length between 300 and 1000 m per day (see Chapter 2). The daily path lengths calculated for red-shanked doucs on Son Tra is within this range. There was no correlation of daily path length with phenology, although sample size is generally too small to evaluate the relationship of daily path length with optimal foraging theory (Clutton-Brock, 1977; McKey & Waterman, 1982). Precipitation was the only variable that significantly influenced daily path length in this study, with smaller path lengths during increases in rainfall.

5.4.7. Interspecific associations

Interspecific associations between doucs and macaques and doucs and muntjacs do not represent stable-mixed interspecific associations, such as those among some colobines (Bshary &

Noe, 1997; Chapman & Chapman, 1996; Chapman & Chapman, 2000b; Mitani, 1991; Wachter et al., 1997; Whitesides, 1989). Sometimes associations simply result from chance encounters relating to similarities in travel paths and feeding trees (Waser, 1982: Waser, 1984; Whitesides, 1989), and this likely explains associations on Son Tra. Regardless, there are peaks in associations implying that associations are not merely the result of habitat size.

The longest douc and macaque associations were in August and October. For August, this month also contains peaks in flowering and fruiting suggesting the availability of high quality foods may permit chance associations to extend over longer time periods. October is characterized by an increased degree of fission-fusion behaviors between units, possibly to reduce the effects of scramble competition (see above). Macaque and douc associations in this month would act to increase competition, thus reducing the foraging benefits of increasing the degree of fission-fusion behaviors.

Chapman & Chapman (2000b) suggested factors influencing interspecific associations vary temporally and between habitats. Therefore, the frequency of associations on Son Tra might fluctuate according to various factors. Among these, associations may provide predator avoidance benefits similar to stable associations in African colobines (Bshary & Noe, 1997; Chapman & Chapman, 1996; Chapman & Chapman, 2000; Wachter et al., 1997). Regarding predation pressures, there are numerous animals on Son Tra which pose a potential threat to primates including eagles (e.g. *Ictinaetus malayensis*, *Nisaetus nipalense*), carnivores (e.g. *Prionailurus bengalensis*) and snakes (e.g. *Bungarus fasciatus*, *Naja kaouthia*, *Ovophis monticola*, *Trimeresurus* spp.).

Associations between doucs and muntjacs were more common during peaks in fruiting. One muntjac was observed to feed on *Lithocarpus fenestratus* seeds dropped by the doucs and another muntjac appeared to feed on *Lithocarpus thomsonii* seeds dropped by the doucs. Therefore, this association provides foraging benefits to muntjacs by allowing them access to otherwise inaccessible foods. Regardless, this association is not stable and is most likely the function of chance encounters.

Similar associations have been described for *Pecari tajacu* and *Alouatta caraya* and *Cebus olivaceus,* where the peccaries fed on fruit dropped by the primates (Desbiez et al., 2010), and between *Presbytis entellus* and *Axis axis*, which feed on vegetation dropped by the langurs (Newton, 1989). These associations provided a foraging benefit and appeared to provide predator detection benefits as the species were observed to react to the alarm calls of one another. In my study the doucs would call in response to the alarm barks from muntjacs.

5.5. Conclusion

The average unit size on Son Tra is 6.5 ± 1.2 individuals. At group scale the average size is 18.0 ± 3.6 individuals, and groups consist of an average of 2.7 ± 0.6 units. Social organization is modular based similar to other odd-nosed colobines, *Papio hamadryas,* and *Homo sapiens*. This consists of units with a daily pattern of fission-fusion. Units were one-male or multi-male, with some resembling monogamous pairs. Group size and social patterns may be influenced by intergroup contest competition and intragroup scramble competition. Vocalizations appear to be very important in coordination between units.

The degree of unit cohesion is better analyzed via observations of fission and fusion as opposed to unit size analyses. Fission-fusion analysis revealed units increase the degree of fission-fusion events between October and December. The number of observed fission-fusion events per month is significantly correlated with precipitation and leaf flush, indicating units are least cohesive in the rain and most cohesive when young leafs are abundant, supporting some influence of scramble competition. This is further supported by hourly analysis of fission and fusion on a seasonal scale for which units fused significantly more during the dry season, and the relationship between the daily pattern of fission and fusion and activity budgets (Chapter 6). Hourly analysis revealed two peaks in daily fission (morning and early afternoon) and two peaks in daily fusion (mid-day and overnight).

The adult male to female sex ratio was 1:1.63 individuals. The adult to subadult to juvenile to infant ratio was 3.7:0.8:0.8:1.5 individuals. The adult to immature ratio is 1.26:1 individuals.

Based on both total and partial unit composition counts, approximately 41% of units were multi-male, indicating multi-male units are regular and stable, and suggesting ecological constraints selecting for the one-male unit are more relaxed. Adult males of one-male units may be of higher quality and preferred by females. Both unit size and unit composition of the main research groups were comparable to other units on Son Tra indicating they are representative.

Home range size of the primary research group was 36.001 ha with a core area of 8.02 ha. Variation in the use of home range tended to increase during the wet season. Overlap in home ranges between adjacent groups appears to be minimal, and the locations where super-trooping events occurred were only along the borders of the home range. The average daily path length was 509.11 ± 244.87 m, with the average dry season daily path length being longer than the wet season daily path length. On a daily scale, day path length was significantly and positively correlated with precipitation, indicating the doucs travel less with increases in rainfall.

Interspecific associations between the doucs and macaques and between doucs and muntjacs peak during the wet season but do not significant correlations with phenology or weather variables. Associations were not stable. Douc and macaque associations have foraging costs to both species, but may have benefits related to increased predator detection. Douc-muntjac associations have foraging benefits for the muntjacs.

Chapter 6. Activity budgets

6.1. Introduction

6.1.1. Chapter preview

Information on *Pygathrix* activity budgets has increased significantly over the last seven years (Ha Thang Long, 2009; Hoang Minh Duc, 2007; Phiapalath, 2009; Rawson, 2009). This introduction reviews our current understanding and the challenges of comparing activity budgets. Methods of evaluation are presented, followed by results which are divided into five sections. Sections one through four of the results analyze activity budgets on the annual, seasonal, monthly, and daily scales. The last section describes copulation and terrestrial observations. Discussions focus on similarities and differences with other colobines, and factors influencing activity patterns.

6.1.2. Review of *Pygathrix* activity budgets

Hoang Minh Duc (2007) reported the annual activity budget in black-shanked doucs as resting (43%), feeding (35%), moving (15%), socializing (6%) and other (1%). Hoang Minh Duc did not record vocalizations or local movements, and "other" behaviors involved more than self-grooming. He did not observe significant differences in the activity budgets between adults and juveniles, or adult males and adult females. During high quality food scarcity (dry season), resting and moving decreased and feeding increased, and during high quality food abundance feeding decreased and resting and moving increased. In males, allogrooming and display behaviors were more common in the dry season. In all individuals, play behaviors and copulation were more common in the wet season. Feeding and moving peaked daily between 6:00 and 8:00, and between 15:00 and 17:00. Resting peaked between 11:00 and 14:00.

Rawson (2009) reported the annual activity budget in black-shanked doucs as inactivity (61%), feeding (27%), travel (7%), social (3%) and other (2%). Categories are identical as in my study, although he included urination, defecation in addition to self-grooming in “other” behaviors. He found resting was the most common inactive behavior (94.2%), allogrooming was the most common social activity (78.9%), self-grooming was the most common “other” behavior (95%), and vocalizations were rarely observed (n=11). Copulation was observed once (wet season). Social behaviors were more common in adult males than females or young individuals, and young individuals traveled more than adults. There were no significant differences between the seasons. Feeding and moving peaked daily between 5:00 and 6:00 and 14:00 and 17:00, and resting peaked between 10:00 and 14:00. Social behaviors tended to peak with inactivity.

Ha Thang Long (2009) and Ha Thang Long et al. (2010) reported activity budgets in grey-shanked doucs as resting (37.0%), traveling (25.8%), socializing (25.1%), feeding (11.9%) and other (0.1%). He included vigilance and self-grooming as forms of socializing. Adult females fed, rested and traveled more than adult males, and adult males were more vigilant. Adults fed more, and socialized and rested less than young individuals. Resting increased and traveling decreased during the wet season, which they suggested relates to food availability. Feeding and traveling peaked during 6:00 and between 16:00 and 17:00. Resting peaked between 9:00 and 10:00, and between 13:00 and 14:00. Social behaviors remained relatively constant throughout the day.

Phiapalath (2009) reported annual activity budgets in adult red-shanked doucs in Laos as feeding (39.5%), inactive/resting (32.7%), traveling (10%), socializing (5%) and other (13.7%). It is unclear if traveling includes local movements, but playing and copulation behaviors were recorded in the category “other”. Self-grooming was the most common “other” behavior

(38.9%), and allogrooming was the most common social behavior (57.7%). Inactivity increased daily between 11:00 and 15:00. Phiapalath & Suwanwaree (2010) reported annual activity budgets of all individual in this same population as feeding (29.5%), inactive/resting (26.2%), and travel/local movements (23.2%), socializing (14.9%) and other (6.4%). In their report, self-grooming and play behaviors were forms of social activity, but they do not define behavioral categories. Self-grooming was the most common social behavior (43.3%). The groups inhabiting the more disturbed forest rested less, and were more vigilant and traveled more compared to the groups in the less disturbed forest. They attributed this to hunting and food scarcity in the dry season, although no statistical quantification is presented to support suggested trends.

Otto (2005) reported on the activity budgets of both grey-shanked and red-shanked doucs over the course of one to 10 days. Her results are reviewed in Chapter 2, but given the presence of more robust data on wild doucs, her results are not compared in this chapter.

6.1.3. Activity budget patterns and comparisons

In *Pygathrix*, the range of percentages for activities vary greatly; resting/inactive behaviors range from 26.2% to 61%, feeding ranges from 11.9% to 39.5%, moving ranges from 7% to 25.8%, and social behaviors range from to 3% to 25.1%. These differences can be related to numerous factors.

Categories used by Rawson (2009) are generally followed in this dissertation, and these are also comparable to Ha Thang Long (2009) with the exception of the subcategory placement of vigilant behaviors. There are differences between the *Pygathrix* studies regarding which activities are recorded in a category, complicating comparisons. Kool (1989) stated that activity budget comparisons are biased due to methodological differences, and due to the affects that group compositions and habitat have on activity patterns. Comparisons made in this study should be regarded within this framework.

6.2. Methods of data analysis

Activity budgets are divided into five mutually exclusive categories including inactive, feeding, moving, social, and other behavior. Behaviors recorded in each category are discussed in Chapter 3. The category “other” only includes self-grooming. Inactive, moving and social behaviors contain subcategories that are analyzed. Not all subcategories or sub-subcategories are analyzed.

“All individuals” refers to adults, subadults, juveniles, infants, and unidentified individuals. “All adults” include adult males and adult females. “Young individuals” refers to subadults, juveniles, and infants. Adults are compared to young individuals, and adult males are compared to adult females.

Of the 30,441 data points collected, both seasons have large sample sizes which reduce seasonal bias: 12,804 dry season and 17,637 wet season data points. Adult males and adult females have large sample sizes, also reducing bias: 14,895 adult male and 10,595 adult female data points. There is an adult bias: 25,482 adult and 3,462 young individual data points.

For 12 month analyses, data collected during the same months in 2010 and 2011 are combined. For annual and seasonal analyses activity budgets are compared using the two-tailed chi-square test (X^2) with Yates’ correction, the contingency coefficient control, and p=0.05. Yates’ correction is used because sample sizes are large. The contingency coefficient (C) was employed on all significant chi-square tests as a means to enhance the statistical tests. Due to the large sample sizes there is an increased likelihood of producing statistically significant results without the existence of a meaningful relationship between the tested variables. This requires a correction factor. The C-value, as a percentage of C-max, allows for an additional measure of the degree of association between variables. In this study, only significant chi-square tests that also have a C-value of 25% (0.25) or greater are considered significant and reported. All other significant chi-square results are not considered significant and are not reported in the text, although they are reported in Table 6.5 at the end of section 6.3.2 of this chapter. A C-value of 25% was chosen because this value has been used in other socioecology primatology studies (Mitani, 1989). Also, this value effectively removes chi-square results which were only significant due to large sample sizes.

For monthly analyses Pearson's Correlation coefficient is used with two-tails and p=0.05. This test is more stringent than other correlations such as Spearman's Rank, and collected data are ratio based.

Non-significant results are generally not presented or illustrated.

6.3. Results

6.3.1. Annual activity budgets

6.3.1.1. All individuals

Activity patterns are illustrated in Figure 6.1, and Table 6.1 provides the percentages and sample sizes. Inactive behavior was the most common behavior (35.3%), followed by moving (28.6%), socializing (21.7%), feeding (13.7%) and other (0.7%).

Figure 6.1. Annual activity budget in all individuals.

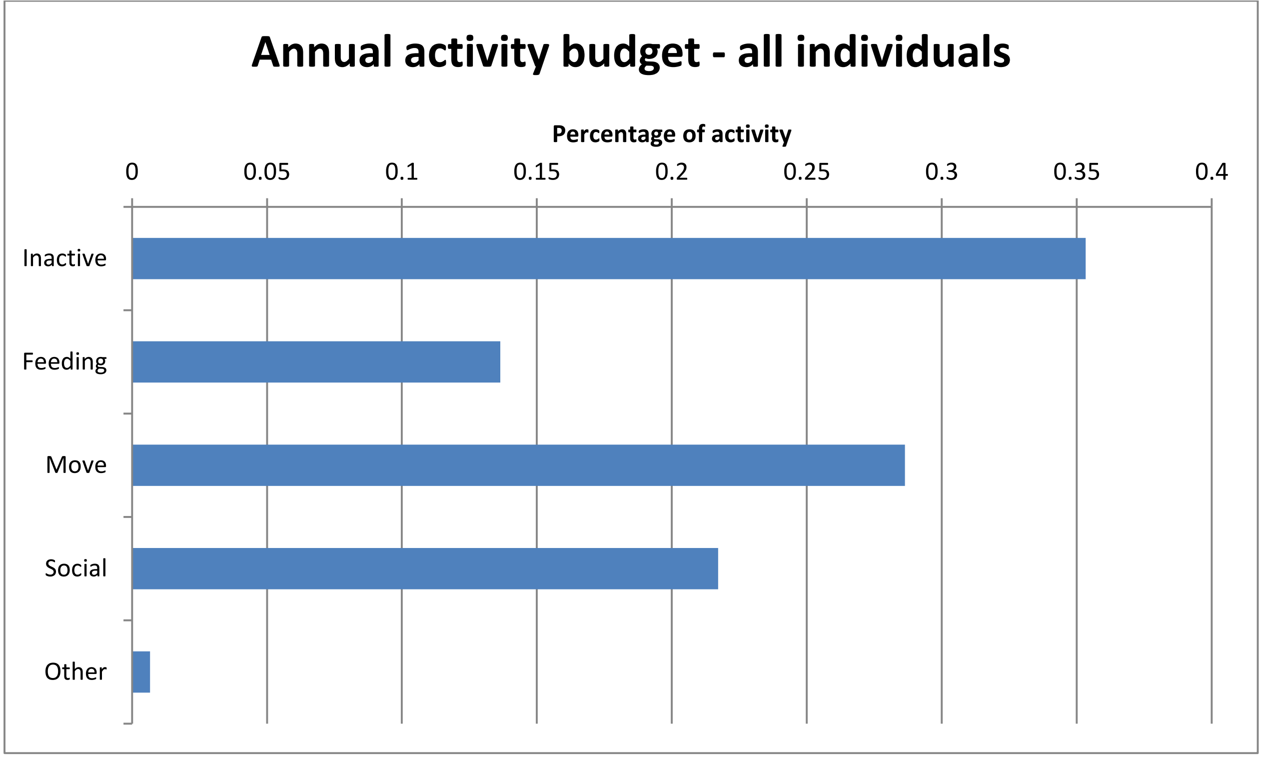


Table 6.1. Annual activity budget: percentages and sample sizes.

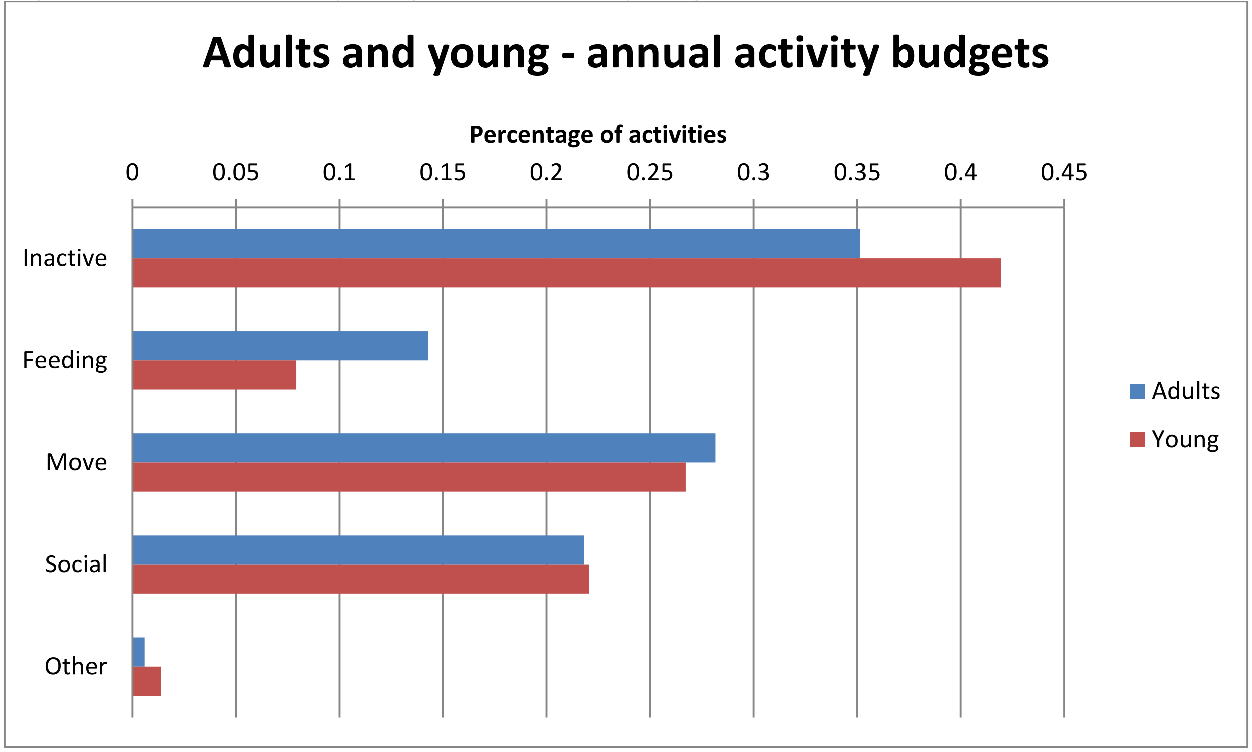
	All individuals		Adults		Young		Adult males		Adult females	
	%	N	%	N	%	N	%	N	%	N
Inactive	35.3	10755	35.1	8954	41.9	1452	34.1	5084	36.6	3875
Feeding	13.7	4155	14.3	3639	7.9	274	12.4	1845	16.9	1794
Moving	28.6	8717	28.2	7177	26.7	925	25.1	3746	32.4	3431
Social	21.7	6609	21.8	5559	22.1	763	27.6	4108	13.7	1454
Other	0.7	205	0.6	153	1.4	48	0.8	112	0.4	41
Total N	30441		25482		3462		14895		10595	

6.3.1.2. Adult and young individuals

Adults and young individuals show the same ranking of activities, but there are different percentages reflecting differences in the frequency of activities. For adults, inactivity was the most common behavior (35.1%), followed by moving (28.2%), socializing (21.8%), feeding (14.3%) and other (0.6%). For young individuals, inactivity was also most common (41.9%), followed by moving (26.7%), social behaviors (22.1%), feeding (7.9%) and other (1.4%).

The annual activity budget of adult and young individuals did not significantly differ. Results that were significant with chi-square but did not reach significance through the contingency coefficient are shown in Table 6.5 at the end of section 6.3.2.

Figure 6.2. Annual activity budget in adults and young individuals.

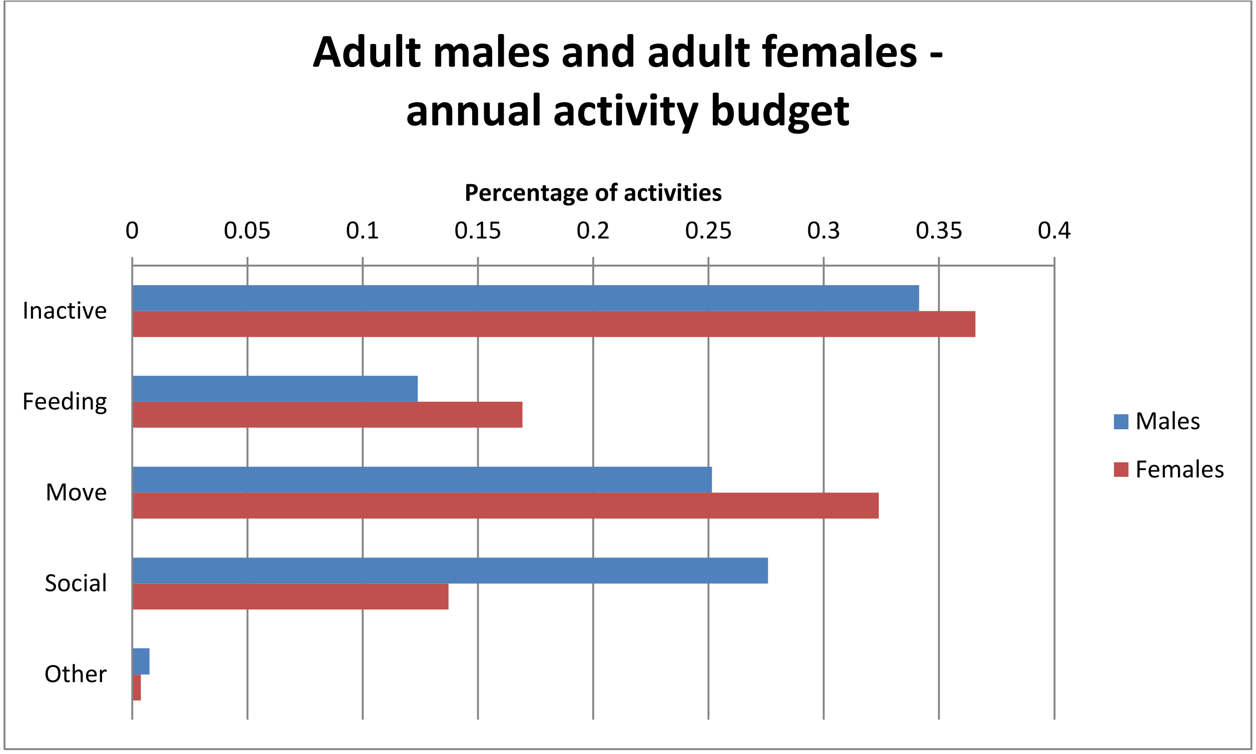


6.3.1.3. Adult males and adult females

Inactivity for adult males was the most common behavior (34.1%), followed by social behaviors (27.6%), moving (25.1%), feeding (12.4%) and other (0.8%). For adult females, inactivity was also the most common behavior (36.6%), followed by moving (32.4%), feeding (16.9%), social activity (13.7%), and other (0.4%). The activity budgets are compared in Figure 6.3.

The annual activity budget of adult males and adult females did not significantly differ. See Table 6.5 at the end of section 6.3.2 for comparisons that did not reach significance through the contingency coefficient.

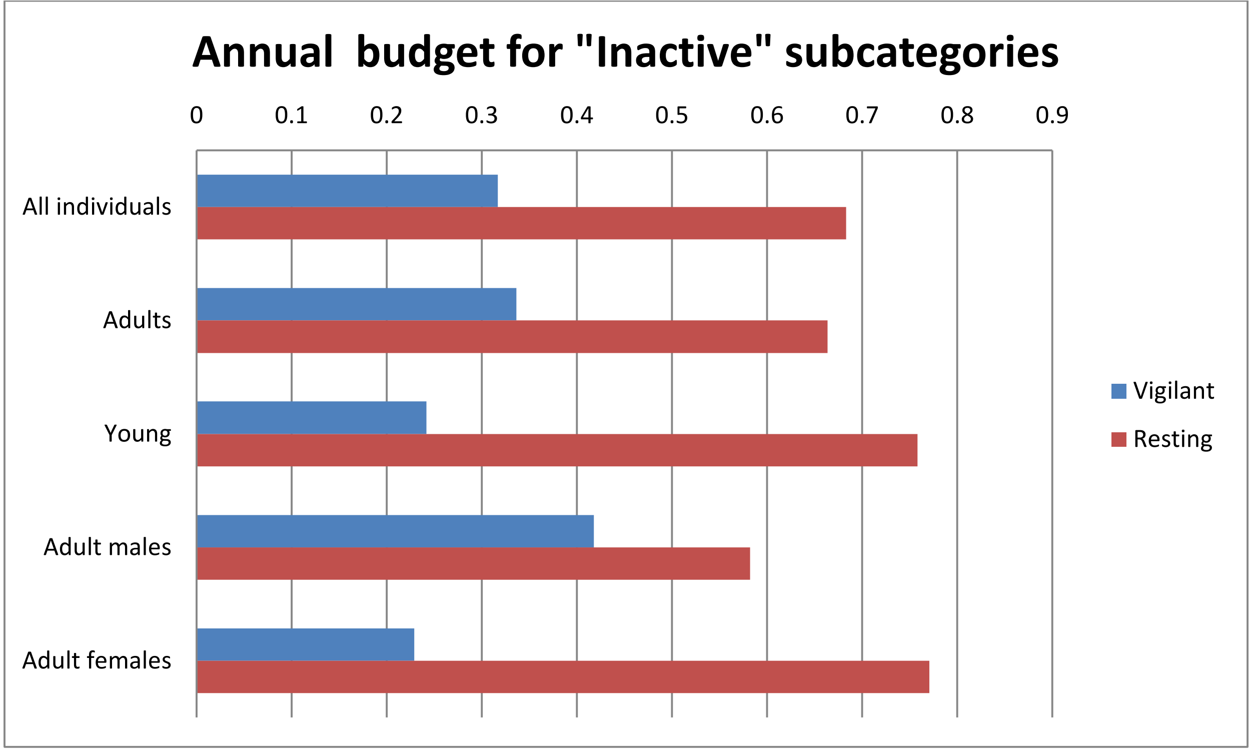
Figure 6.3. Annual activity budget in adult males and adult females.



6.3.1.4. Annual "inactive" behaviors

There are two subcategories in "inactive" behaviors (vigilance and resting), and therefore percentages of these subcategories are inverses and the chi-square results for vigilance are identical to the results for resting. Vigilance accounted for 31.7% of inactive behavior in all individuals, 33.6% in adults, 24.2% in young individuals, 22.9% in adult females, and 41.8% in adult males (Figure 6.4 and Table 6.2). Adults males were significantly more vigilant than adult females [$X^2(1, N=10406) = 349.71$ $p<0.0001$, C=0.26], and the inverse is also significant indicating adult females rest significantly more than adult males. See Table 6.5 at the end of section 6.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

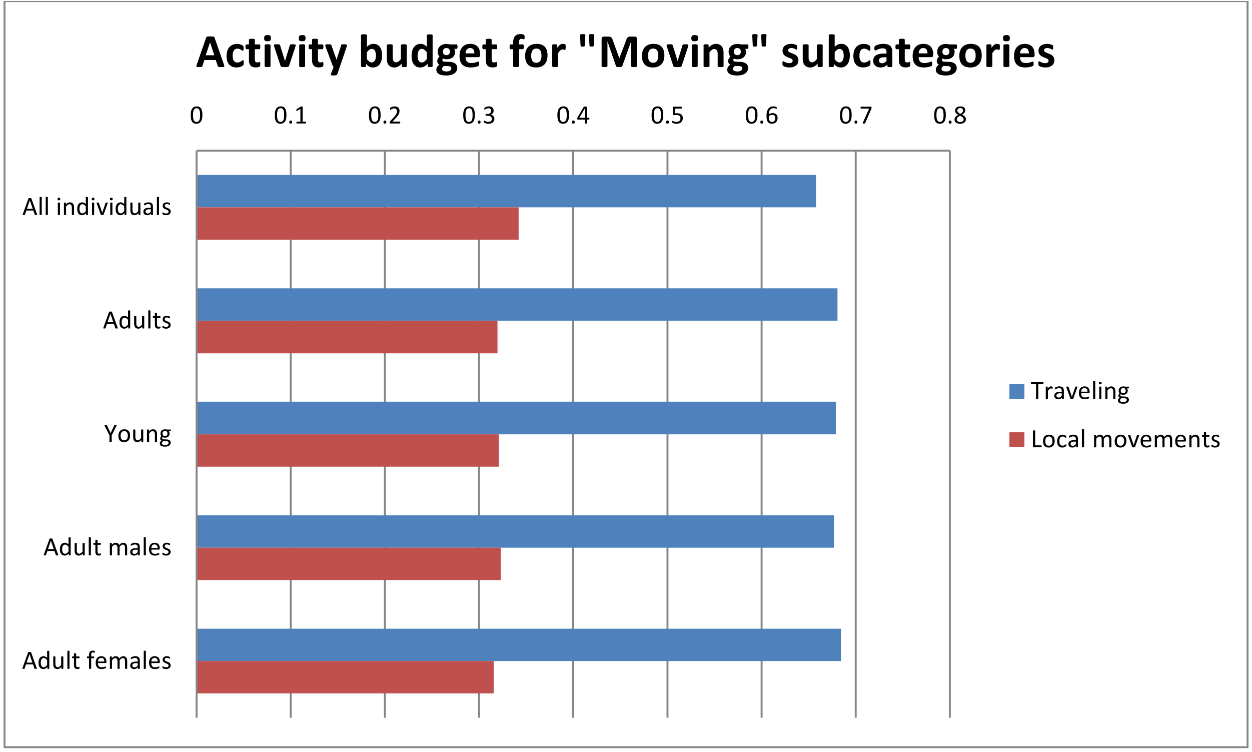
Figure 6.4. Annual activity budget of inactive behavior subcategories (resting and vigilance).



6.3.1.5. Annual “moving” behaviors

There are two subcategories in “moving” behaviors (traveling and local movements), and therefore percentages of the subcategories are inverses and the chi-square results for traveling are identical to results for local movements. Traveling accounted for 65.8% of moving behaviors in all individuals, 68.1% in adults, 67.9% in young individuals, 68.4% in adult females, and 67.7% in adult males (Figure 6.5 and Table 6.2). Moving subcategories were not significantly different between adults and young individuals, or adult males and females.

Figure 6.5. Annual activity budget of moving behavior subcategories (traveling and local movements).



6.3.1.6. Annual "social" behaviors

Social behaviors are here divided into five subcategories and illustrated in Figure 6.6 and Table 6.2 (displaying, vocalizing, grooming, playing, and copulating). Copulation is reviewed in the fifth section of this chapter.

Young individuals played significantly more than adults, and adults vocalized significantly more than young individuals: playing [$X^2(1, N=6326) = 3052.01$, $p<0.0001$, C=0.81], and vocalizing [$X^2(1, N=6326) = 1838.17$, $p<0.0001$, C=0.67].

Adult females allogroomed significantly more than adult males [$X^2(1, N=5562) =259.54$, $p<0.0001$, C=0.30].

See Table 6.5 at the end of section 6.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Figure 6.6. Annual activity budget of social behavior subcategories.

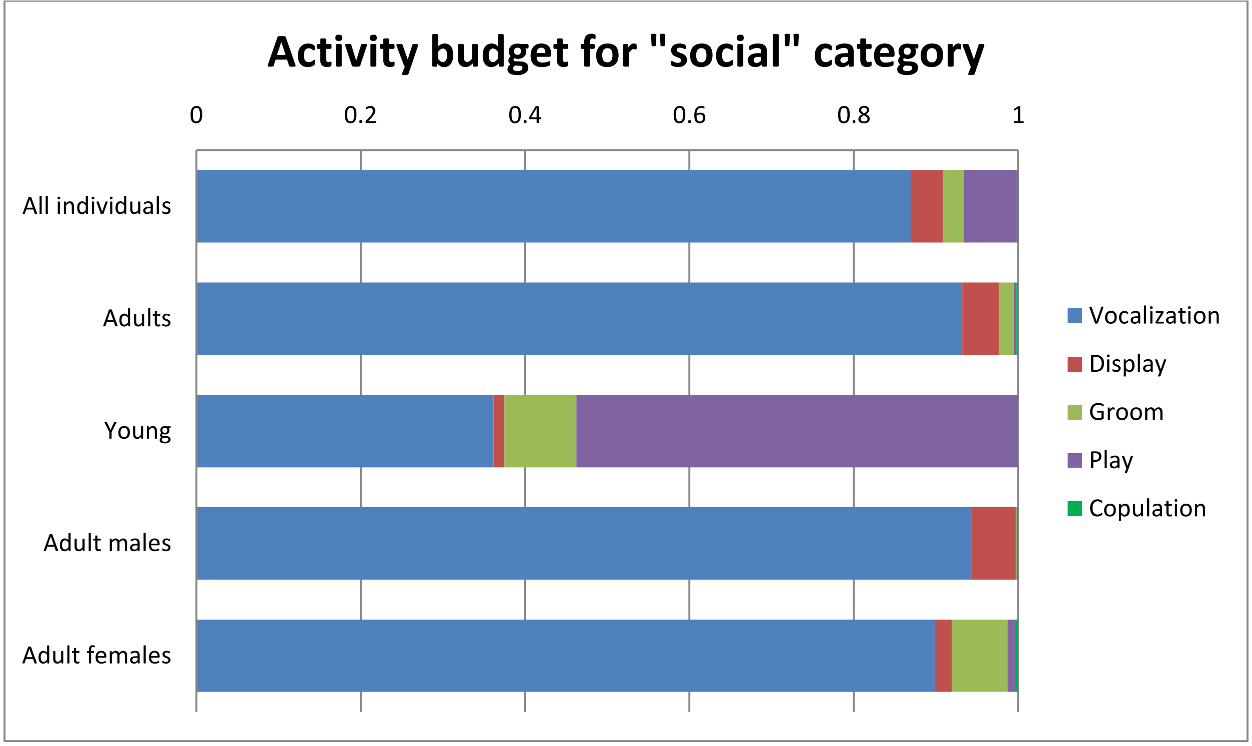


Table 6.2. Annual activity budget of inactive, moving, and social subcategories.

	All individuals		Adults		Young		Adult males		Adult females	
	%	N	%	N	%	N	%	N	%	N
Inactive										
Rest	68.3	7346	66.4	5942	75.8	1101	58.2	2960	77.1	2987
Vigilant	31.7	3409	33.6	3012	24.2	351	41.8	2124	22.9	888
Move										
Travel	5734	65.8	4884	68.1	628	67.9	2536	67.7	2348	68.4
Local	2983	34.2	2293	31.9	297	32.1	1210	32.3	1083	31.6
Social										
Display	3.9	260	4.5	250	1.3	10	5.3	220	2.1	30
Groom	2.6	169	1.8	102	8.8	67	0.1	4	6.7	98
Play	6.4	425	0.3	15	53.7	410	0.1	2	0.9	13
Vocalize	86.9	5746	93.2	5183	36.2	276	94.3	3876	89.9	1307
Copulate	0.2	12	0.2	12	0	0	0.2	6	0.4	6

6.3.2. Seasonal activity budgets

6.3.2.1. All individuals

Wet and dry season activity budgets for all individuals are presented in Figure 6.7 and Table 6.3. There were no significant differences between the seasons for any activity. See Table

6.5 at the end of section 6.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Figure 6.7. Seasonal activity budget in all individuals.

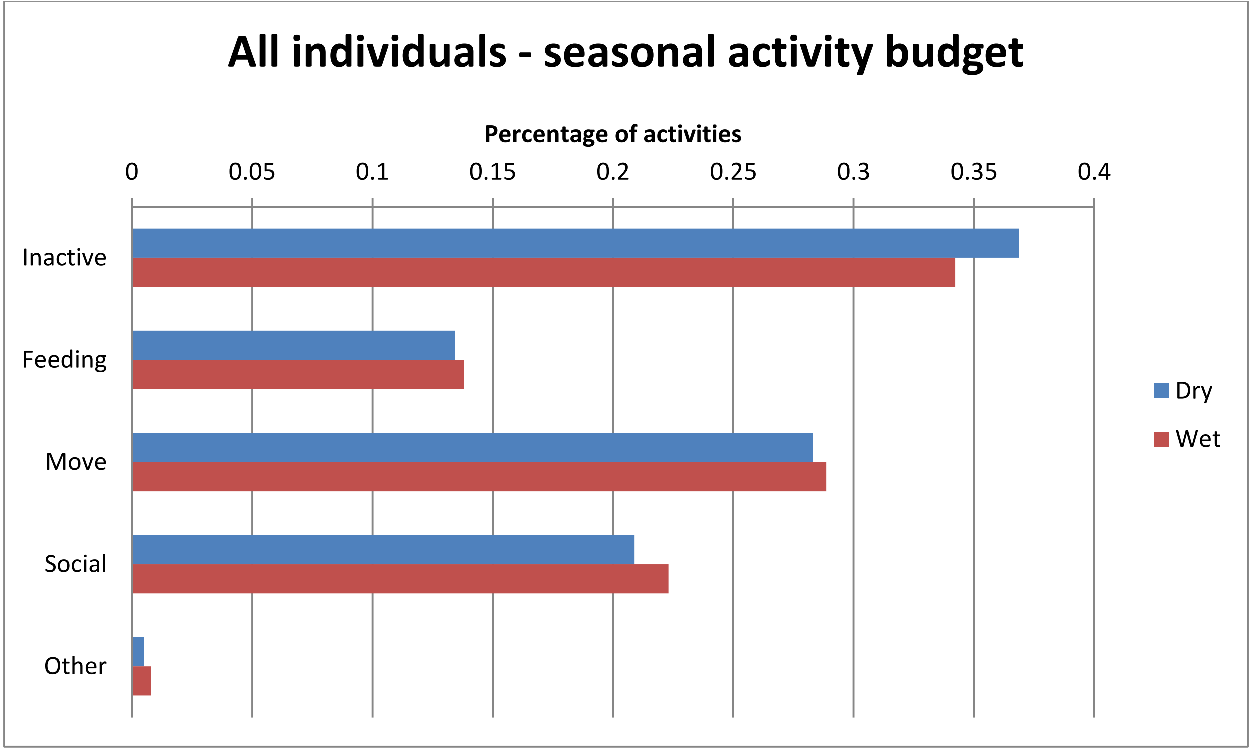


Table 6.3. Seasonal activity budget: percentages and sample sizes.

DRY SEASON (February through May)										
	All individuals		Adults		Young		Adult males		Adult females	
	%	N	%	N	%	N	%	N	%	N
Inactive	36.9	4720	37.9	4025	42.3	657	35.6	2189	41.0	1836
Feeding	13.4	1720	13.2	1402	11.2	174	11.6	712	15.4	690
Moving	28.3	3626	26.1	2774	31.9	495	23.2	1423	30.1	1351
Social	20.9	2674	22.3	2368	13.7	212	28.9	1769	13.4	600
Other	0.5	64	0.5	49	0.9	14	0.7	44	0.1	5
WET SEASON (June through January)										
	All individuals		Adults		Young		Adult males		Adult females	
	%	N	%	N	%	N	%	N	%	N
Inactive	34.2	6035	33.2	4929	41.6	795	33.1	2895	33.4	2039
Feeding	13.8	2435	15.0	2237	5.2	100	12.9	1133	18.1	1104
Moving	28.9	5091	29.6	4403	22.5	430	26.5	2323	34.0	2080
Social	22.3	3935	21.5	3191	28.9	551	26.7	2339	13.9	854
Other	0.8	141	0.7	104	1.8	34	0.8	68	0.6	36

6.3.2.2. Adult and young individuals

Seasonal activity budgets in adults are shown in Figure 6.8 and Table 6.3. There were no significant different between seasons.

Seasonal activity budgets in young individuals are shown in Figure 6.9 and Table 6.3. Social behaviors were significantly more common in the wet season [$X^2(1, N=3462) = 114.08$, $p<0.0001$, C=0.25].

See Table 6.5 at the end of section 6.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Figure 6.8. Seasonal activity budget in adults.

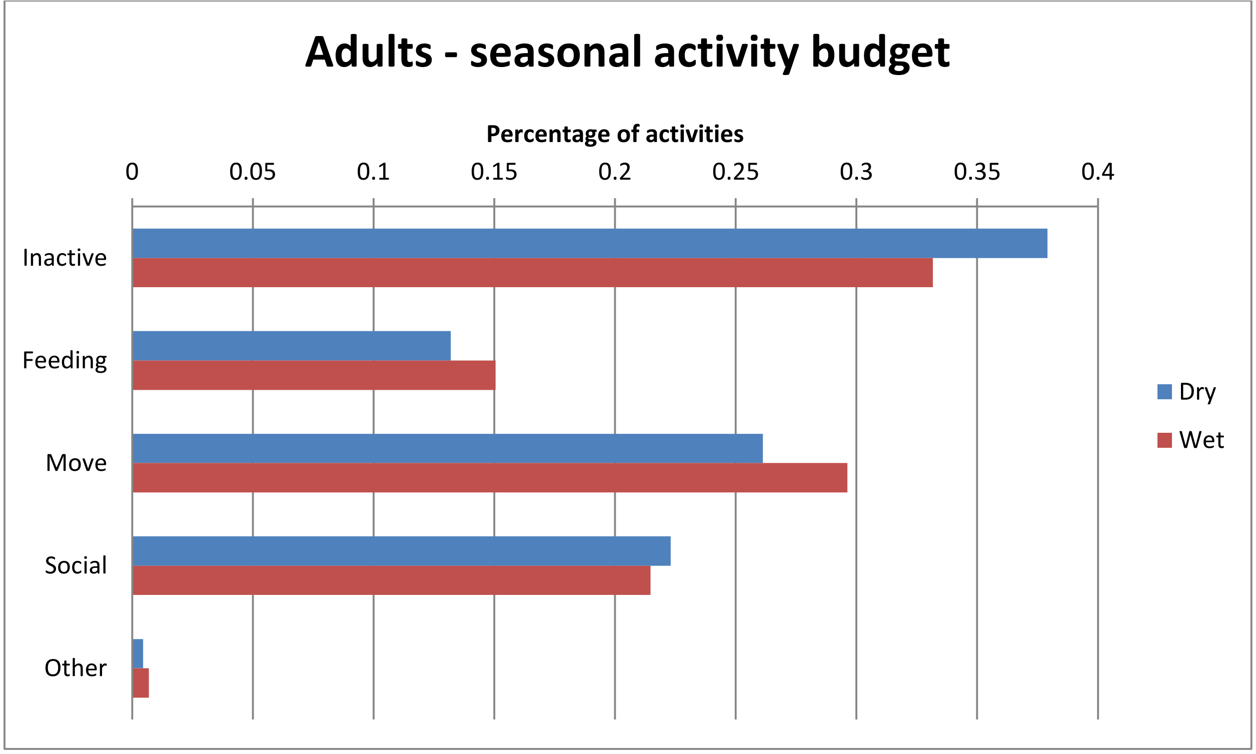
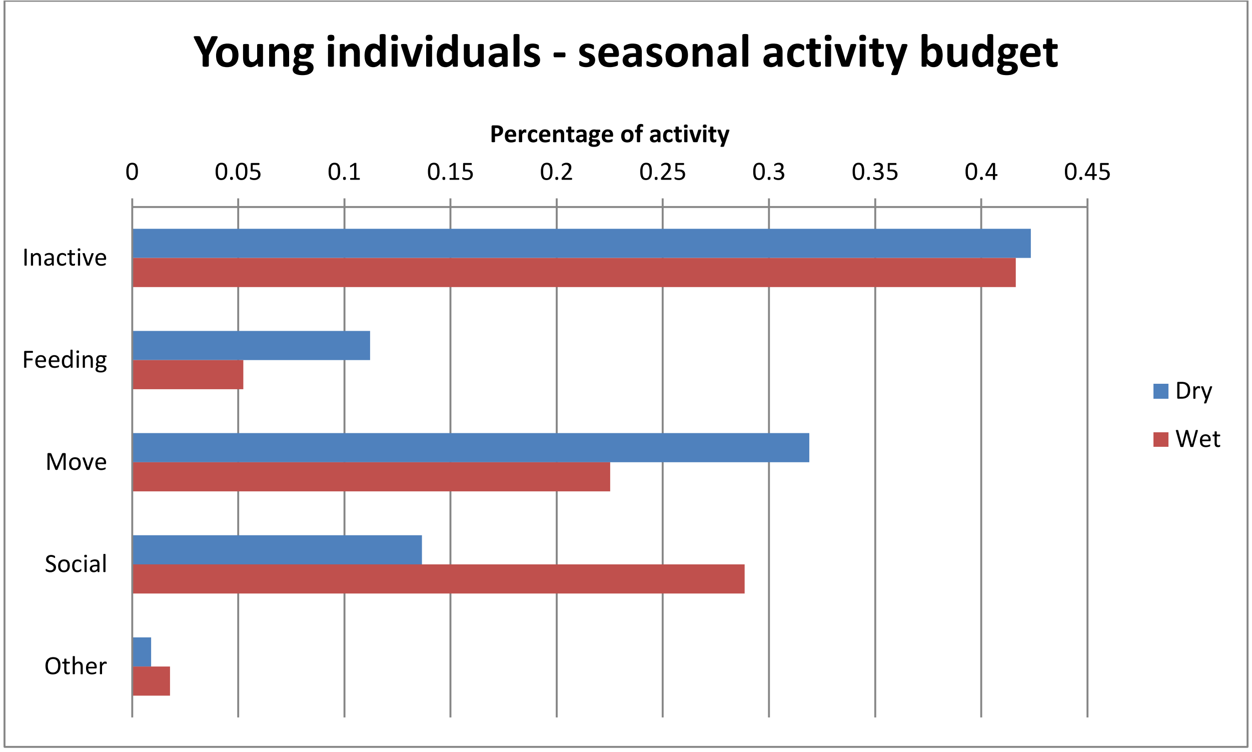


Figure 6.9. Seasonal activity budget in young individuals.



6.3.2.3. Comparing adult and young individuals

Adult and young individuals did not significantly differ in any activity in the dry season (Figure 6.10) or the wet season (Figure 6.11). See Table 6.5 at the end of section 6.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Figure 6.10. Dry season activity budget in adults and young individuals.

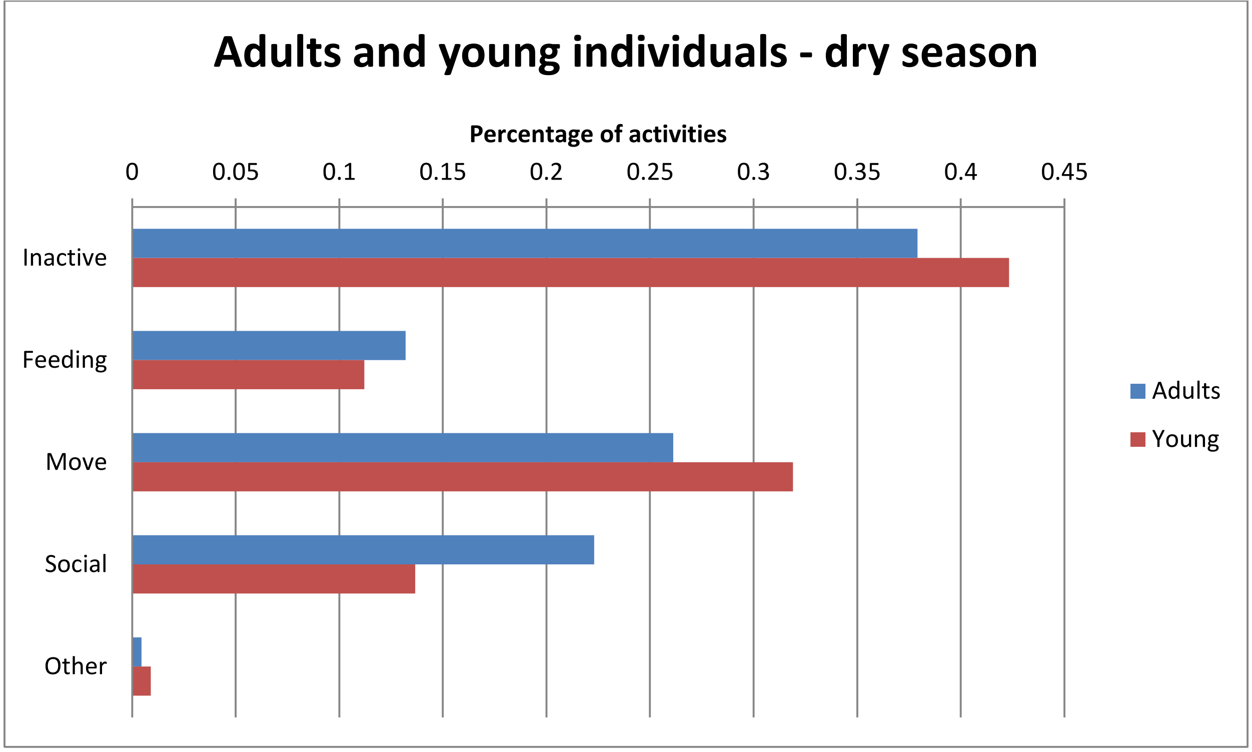
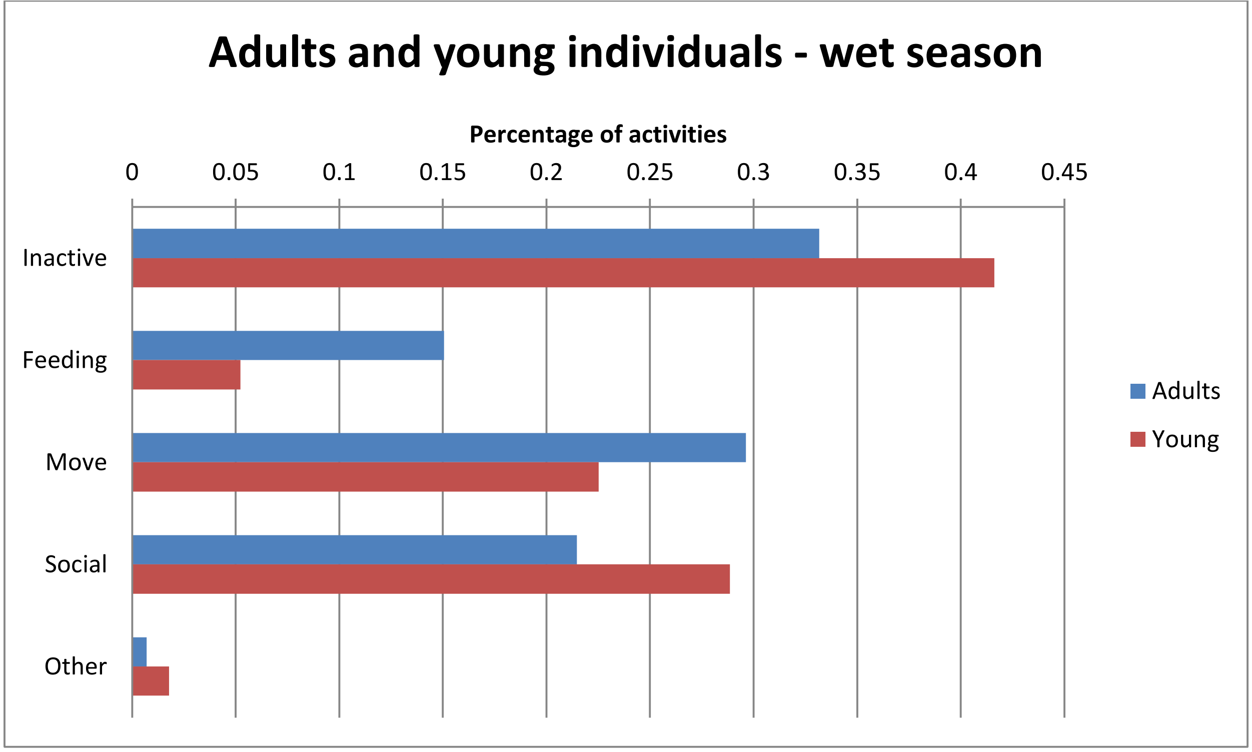


Figure 6.11. Wet season activity budget in adults and young individuals.



6.3.2.4. Adult males and adult females

Seasonal activity budgets in adult males are shown in Figure 6.12 and Table 6.3, and seasonal activity budgets in adult females are shown in Figure 6.13 and Table 6.3. There were no significant differences in activity between seasons for both adult males and adult females. See Table 6.5 at the end of section 6.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Figure 6.12. Seasonal activity budget in adult males.

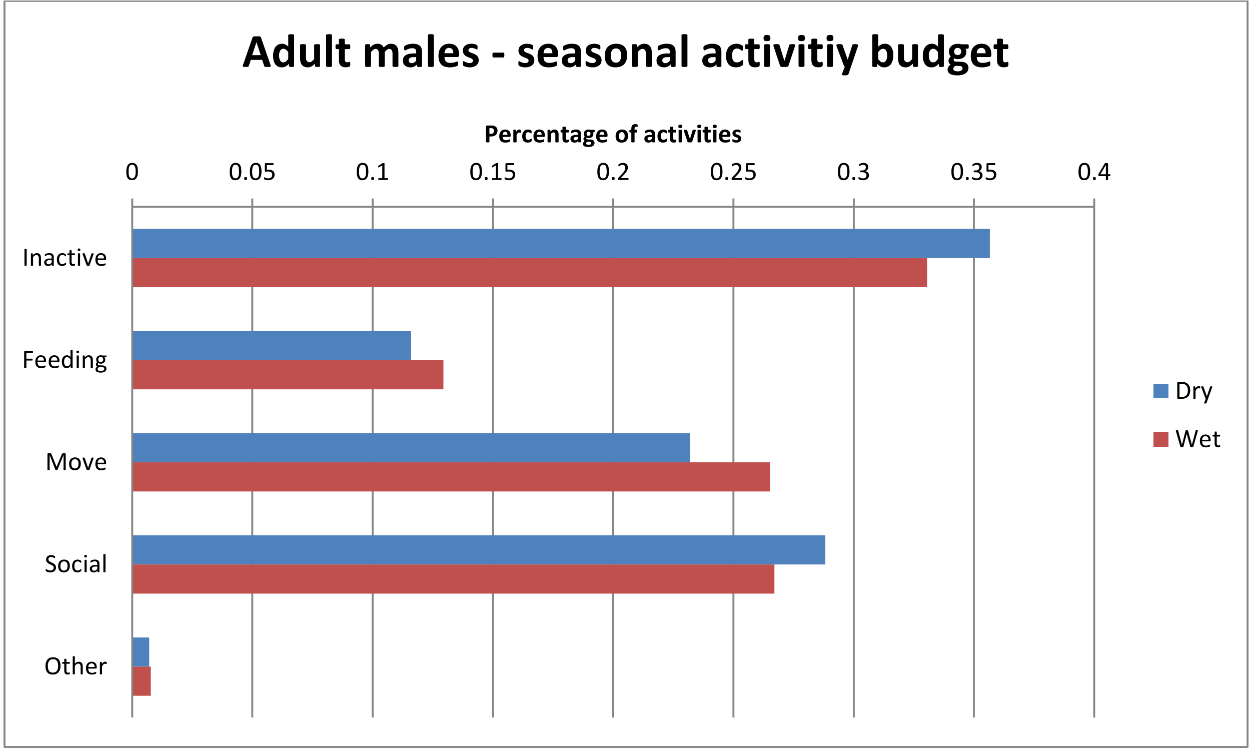
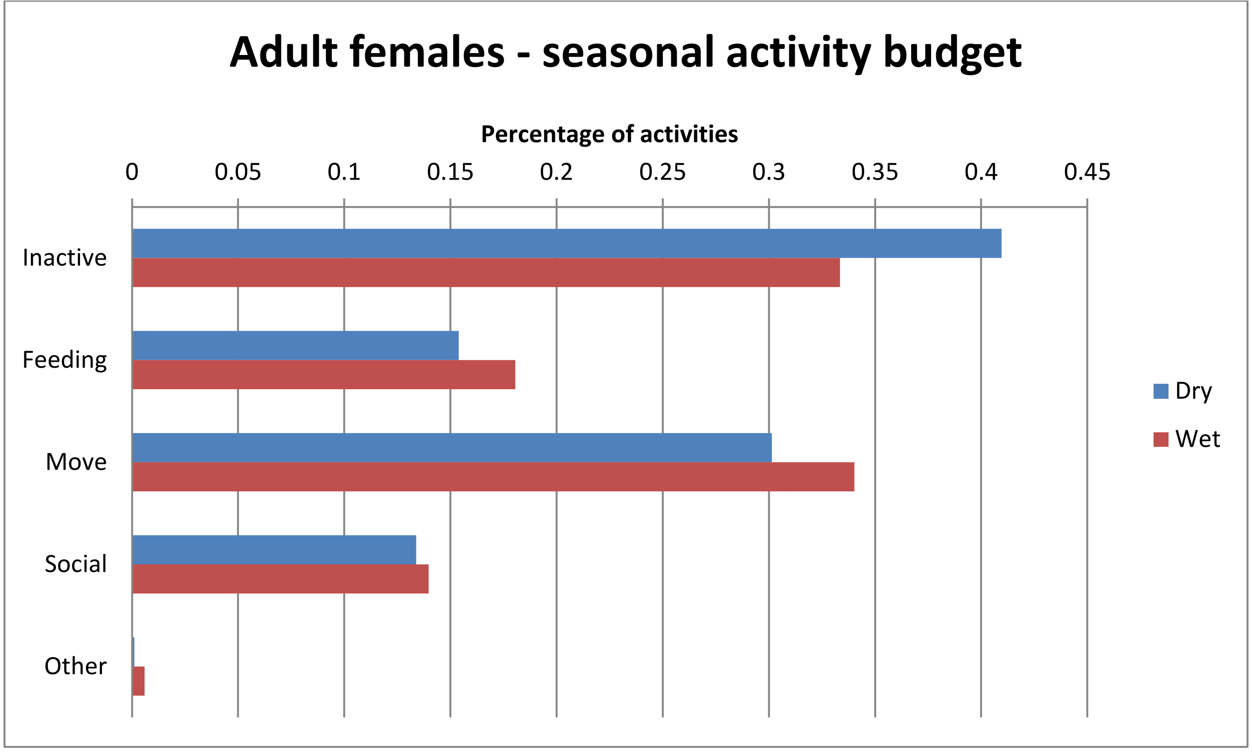


Figure 6.13. Seasonal activity budget in adult females.



6.3.2.5. Comparing adult males and adult females

In the dry season (Figure 6.14) adult males were significantly more social than adult females [$X^2(1, N=10619) = 355.31$, $p<0.0001$, C=0.26]. There were no other significant differences in either the dry season or wet season (Figure 6.15) between adult males and adult females. See Table 6.5 at the end of section 6.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Figure 6.14. Dry season activity budget in adult males and adult females.

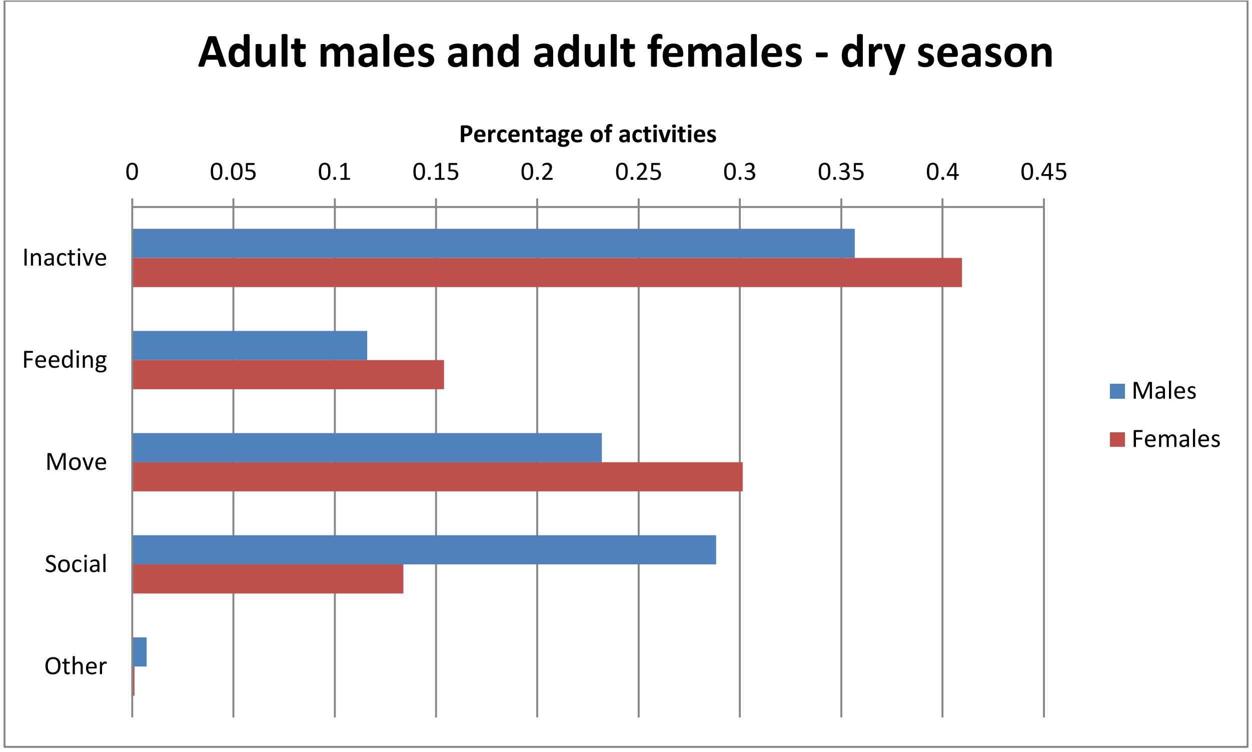
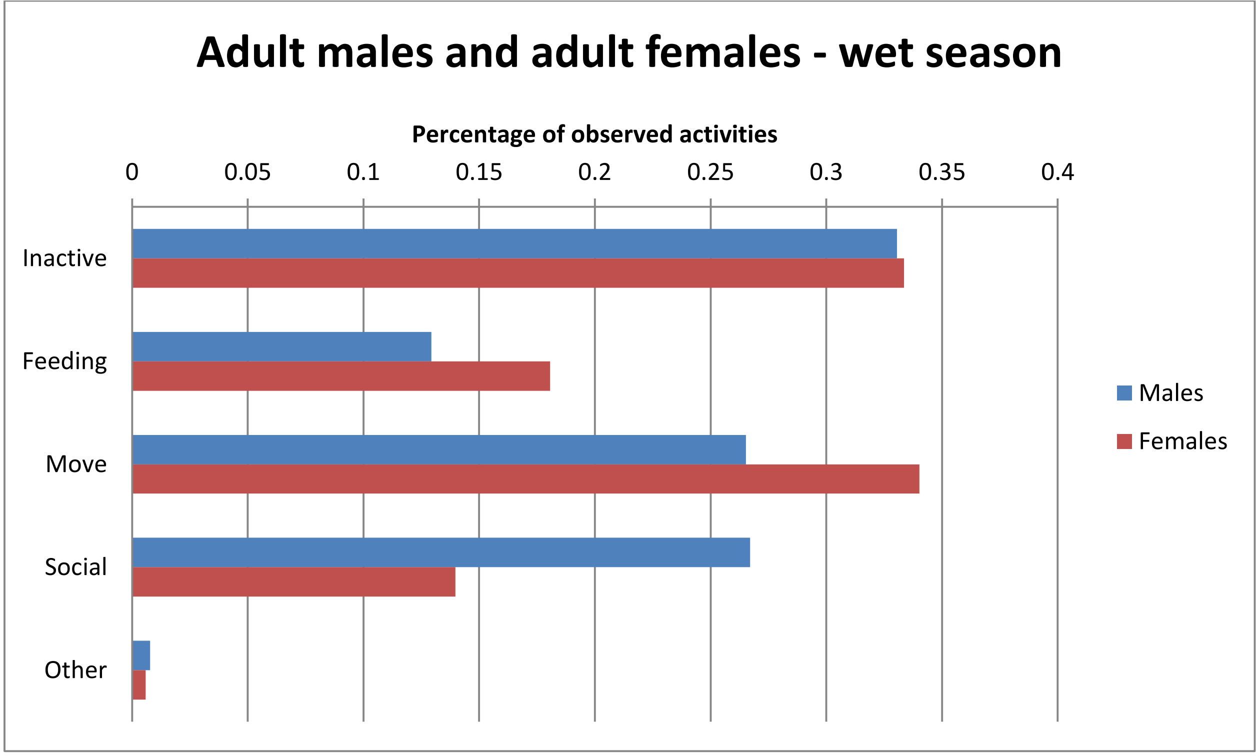


Figure 6.15. Wet season activity budget in adult males and adult females.

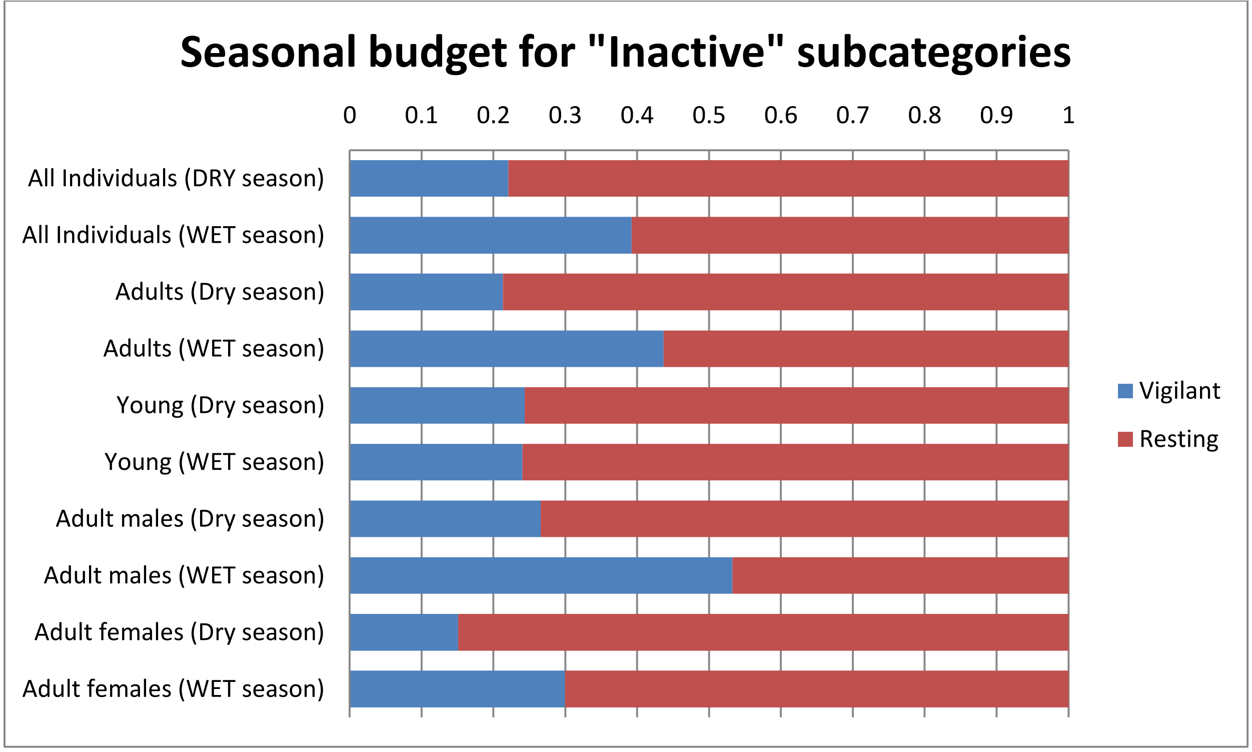


6.3.2.6. Seasonal “inactive” behaviors

There are two subcategories in “inactive” behavior (vigilance and resting), and therefore percentages are inverses and the chi-square results for vigilance are identical to results for resting. Percentages and sample sizes are shown in Figure 6.16 and Table 6.4.

In the wet season adult males were significantly more vigilant than adult females [X^2(1, *N*=4934) = 263.1, p<0.0001, C=0.32]. There were no other significant differences between adult males and adult females, or between adults and young individuals. See Table 6.5 at the end of section 6.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Figure 6.16. Seasonal activity budget in inactive subcategories.

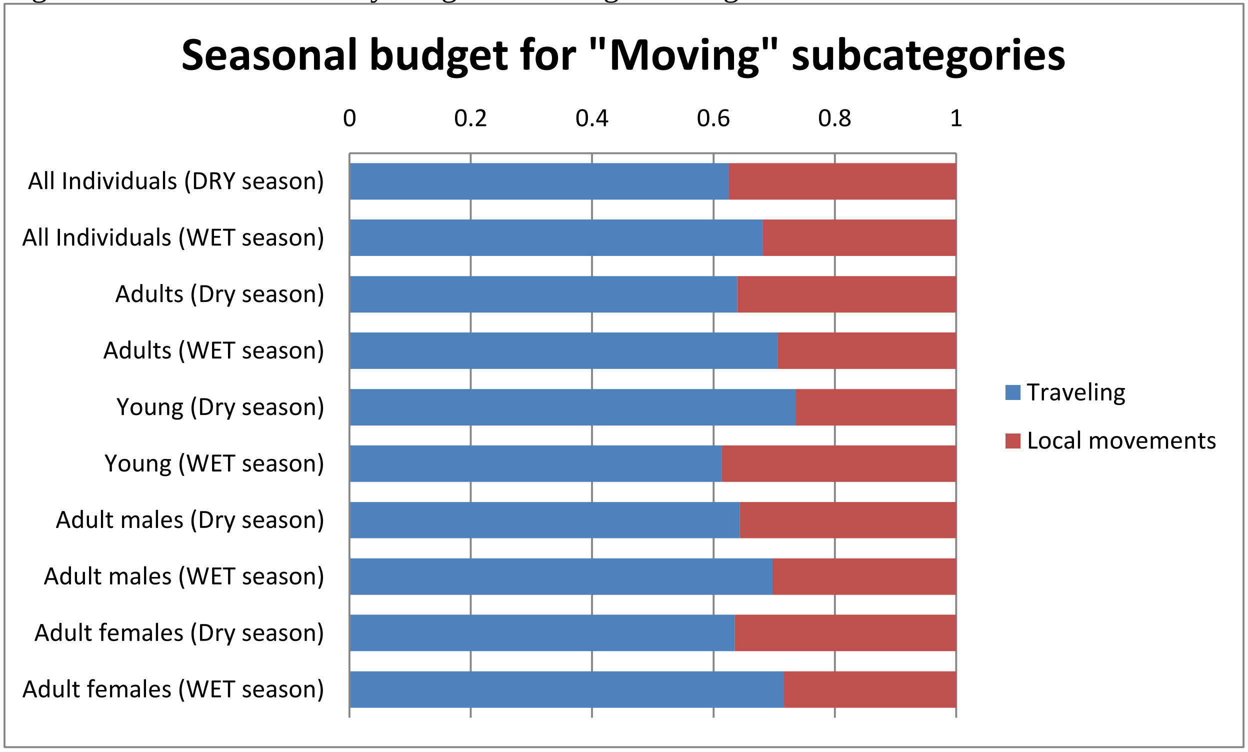


6.3.2.7. Seasonal “moving” behaviors

There are two subcategories in “moving” behavior (travel and local movement), and therefore percentages are inverses and the chi-square results for travel are identical to results for local movements. Percentages and sample sizes are shown in Figure 6.17 and Table 6.4.

There were no significant differences in the frequency of travel or local movements between the wet and dry season in any grouping of individuals. There were also no significant seasonal differences in the frequency of travel or local movements between adult and young individuals, and adult males and adult females during either the wet or dry season. See Table 6.5 at the end of section 6.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Figure 6.17. Seasonal activity budget in moving subcategories.



6.3.2.8. Seasonal “social” behaviors

Social behaviors are divided into five subcategories and illustrated in Figure 6.18 and Table 6.4. Copulation is reviewed in the fifth section of this chapter.

There were no significant differences in social behaviors between seasons in any grouping of individuals.

In the dry season, adults vocalized significantly more than young individuals, and young individuals played significantly more than adults: vocalizing [$X^2(1, N=2580) = 757.08$, $p<0.0001$, $C=0.67$], and playing [$X^2(1, N=2580) = 1428.7$, $p<0.0001$, $C=0.84$]. There were no differences between adult males and adult females.

In the wet season, adults again vocalized significantly more than young individuals, and young individuals played significantly more than adults. Also, adult females allogroomed significantly more than adult males: vocalizing [$X^2(1, N=3746) = 1056.29$, $p<0.0001$, $C=0.66$], playing [$X^2(1, N=3746) = 1683.18$, $p<0.0001$, $C=0.79$], and allogrooming [$X^2(1, N=3193) = 242.24$, $p<0.0001$, $C=0.38$]. See Table 6.5 at the end of section 6.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Figure 6.18. Seasonal activity budget in social subcategories.

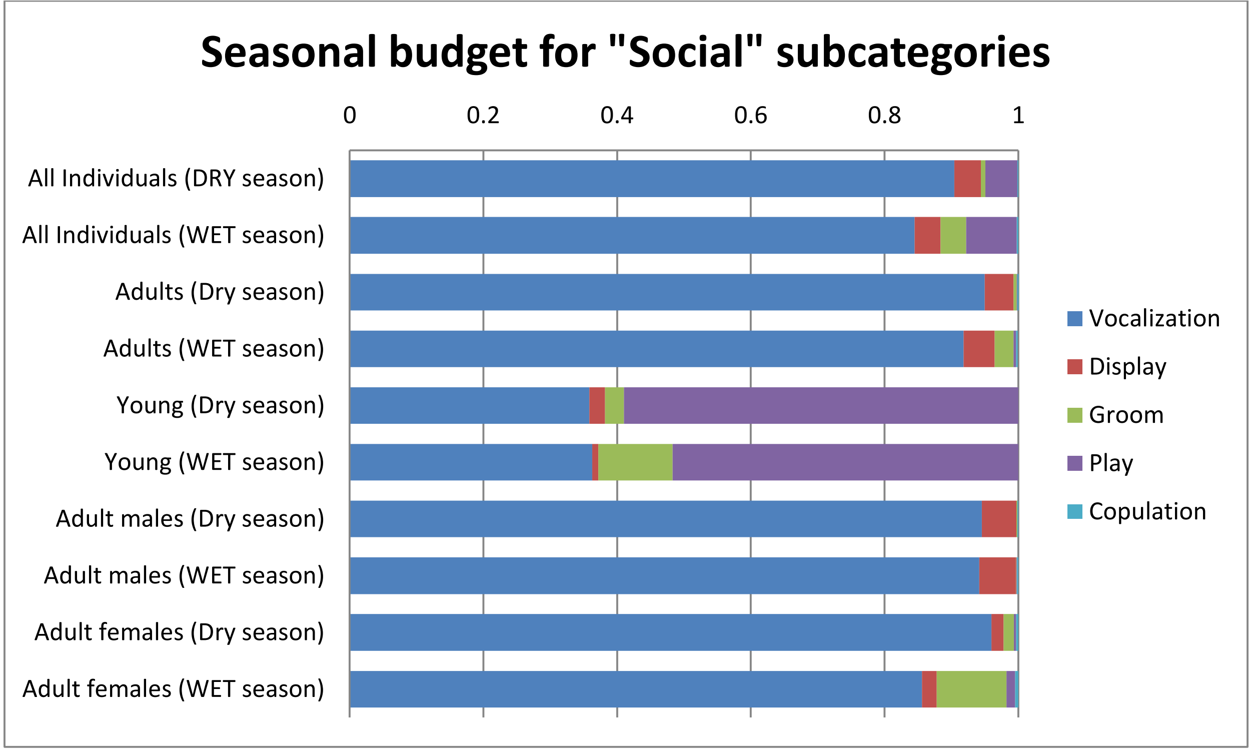


Table 6.4. Seasonal activity budget in inactive, moving, and social subcategories.

DRY SEASON (February through May)										
	All individuals		Adults		Young		Adult males		Adult females	
	%	N	%	N	%	N	%	N	%	N
Inactive										
Rest	77.9	3679	78.7	3166	75.6	497	73.4	1607	84.9	1559
Vigilant	22.1	1041	21.3	859	24.4	160	25.6	582	15.1	277
Move										
Travel	62.5	2268	63.9	1774	73.5	364	64.4	916	63.5	858
Local	37.5	1358	36.1	1000	26.5	131	35.6	507	36.5	493
Social										
Display	4.0	107	4.3	102	2.4	5	5.1	91	1.9	11
Groom	0.7	18	0.5	12	2.8	6	0.2	3	1.5	9
Play	4.7	127	0.1	2	58.9	125	0.0	0	0.3	2
Vocalize	90.4	2419	94.9	2249	35.9	76	94.6	1673	96.0	576
Copulate	0.2	4	0.2	4	0.0	0	0.1	2	0.3	2
WET SEASON (June through January)										
	All individuals		Adults		Young		Adult males		Adult females	
	%	N	%	N	%	N	%	N	%	N
Inactive										
Rest	60.1	3667	56.3	2776	76.0	604	46.7	1353	70.0	1428
Vigilant	39.2	2368	43.7	2153	24.0	191	53.3	1542	30.0	611
Move										
Travel	68.1	3466	70.6	3110	61.4	264	69.7	1620	71.6	1490

Local	31.9	1625	29.4	1293	38.6	166	30.3	703	28.4	590
Social										
Display	3.9	153	4.7	148	0.9	5	5.5	129	2.2	19
Groom	3.8	151	2.8	90	11.1	61	0.1	1	10.4	89
Play	7.6	298	0.4	13	51.7	285	0.1	2	1.3	11
Vocalize	84.5	3327	91.8	2934	36.3	200	94.1	2203	85.6	731
Copulate	0.2	8	0.3	8	0.0	0	0.2	4	0.5	4

Table 6.5. Significant chi-square results and significant contingency coefficient results.

Section number	Variables compared (Frequency of:)	X^2 results	C-value	Significant
6.3.1.2.	inactivity b/t adult and young individuals	(1, N=28944) = 60.96, p<0.0001	0.06	N
	feeding b/t adult and young individuals	(1, *N*=28944) = 105.11, p<0.0001	0.09	N
	other b/t adult and young individuals	(1, *N*=28944) = 26.18, p<0.0001	0.04	N
6.3.1.3.	inactivity b/t adult males and adult females	(1, *N*=25490) = 16.09, p<0.0001	0.04	N
	feeding b/t adult males and adult females	(1, *N*=25490) = 104.17, p<0.0001	0.09	N
	moving b/t adult males and adult females	(1, *N*=25490) = 159.8, p<0.0001	0.11	N
	socializing b/t adult males and adult females	(1, *N*=25490) = 695.99, p<0.0001	0.23	N
	other b/t adult males and adult females	(1, *N*=25490) = 13.22, p=0.0003	0.03	N
6.3.1.4.	vigilance b/t adult and young individuals	(1, *N*=10406) = 50.74, p<0.0001	0.10	N
	vigilance b/t adult males and adult females	(1, *N*=10406) = 349.71 p<0.0001	0.26	Significant
6.3.1.6.	play b/t adult and young individuals	(1, *N*=6326) = 3052.01, p<0.0001	0.81	Significant
	allogroom b/t adult and young individuals	(1, *N*=6326) =121.9, p<0.0001	0.19	N
	vocalizing b/t adult and young individuals	(1, *N*=6326) = 1838.17, p<0.0001	0.67	Significant
	displaying b/t adult and young individuals	(1, *N*=6326) = 16.46, p<0.0001	0.07	N
	play b/t adult males and adult females	(1, *N*=5562) = 25.48, p<0.0001	0.10	N

	allogroom b/t adult males and adult females	(1, *N*=5562) =259.54, $p<0.0001$	0.30	Significant
	vocalizing b/t adult males and adult females	(1, *N*=5562) = 32.98, $p<0.0001$	0.11	N
	displaying b/t adult males and adult females	(1, *N*=5562) = 26.35, $p<0.0001$	0.10	N
6.3.2.1.	inactivity b/t wet and dry seasons in all individuals	(1, *N*=30441) = 22.61, $p=0.0002$	0.04	N
	socializing b/t wet and dry seasons in all individuals	(1, *N*=30441) = 8.8, $p=0.003$	0.02	N
	other b/t wet and dry seasons in all individuals	(1, *N*=30441) = 9.51, $p=0.002$	0.02	N
6.3.2.2.	inactivity b/t wet and dry seasons in adults	(1, *N*=25482) = 31.02, $p<0.0001$	0.05	N
	other b/t wet and dry seasons in adults	(1, *N*=25482) = 5.5, $p=0.02$	0.02	N
	feeding b/t wet and dry seasons in adults	(1, *N*=25482) = 17.09, $p<0.0001$	0.04	N
	moving b/t wet and dry seasons in adults	(1, *N*=25482) = 37.35, $p<0.0001$	0.05	N
	feeding b/t wet and dry seasons in young	(1, *N*=3462) = 41.14, $p<0.001$	0.15	N
	moving b/t wet and dry seasons in young	(1, *N*=3462) = 38.01, $p<0.0001$	0.15	N
	socializing b/t wet and dry seasons in young	(1, *N*=3462) = 114.08, $p<0.0001$	0.25	Significant
	other b/t wet and dry seasons in young	(1, *N*=3462) = 4.21, $p=0.04$	0.05	N
6.3.2.3.	inactivity b/t adults and young in the dry season	(1, *N*=12170) = 11.02, $p=0.0009$	0.04	N
	feeding b/t adults and young in the dry season	(1, *N*=12170) = 4.59, $p=0.03$	0.03	N
	other b/t adults and young in the dry season	(1, *N*=12170) = 4.28, $p=0.04$	0.03	N
	moving b/t adults and young in the dry season	(1, *N*=12170) = 22.65, $p<0.0001$	0.06	N
	socializing b/t adults and young in the dry season	(1, *N*=12170) = 60.02, $p<0.0001$	0.10	N
	inactivity b/t adults and young in the wet season	(1, *N*=16774) = 53.54, $p<0.0001$	0.08	N

	feeding b/t adults and young in the wet season	(1, *N*=16774) = 135.13, p<0.0001	0.13	N
	other b/t adults and young in the wet season	(1, *N*=16774) = 22.91, p<0.0001	0.05	N
	moving b/t adults and young in the wet season	(1, *N*=16774) = 41.36, p<0.0001	0.07	N
	socializing b/t adults and young in the wet season	(1, *N*=16774) = 52.77, p<0.0001	0.08	N
6.3.2.4.	inactivity b/t wet and dry seasons in adult males	(1, *N*=14895) = 10.85, p=0.001	0.04	N
	socializing b/t wet and dry seasons in adult males	(1, *N*=14895) = 8.0, p=0.005	0.03	N
	feeding b/t wet and dry seasons in adult males	(1, *N*=14895) = 5.8, p=0.02	0.03	N
	moving b/t wet and dry seasons in adult males	(1, *N*=14895) = 21.17, p<0.0001	0.05	N
	inactivity b/t wet and dry seasons in adult females	(1, *N*=10595) = 64.21, p<0.0001	0.11	N
	feeding b/t wet and dry seasons in adult females	(1, *N*=10595) = 12.87, p=0.0003	0.05	N
	moving b/t wet and dry seasons in adult females	(1, *N*=10595) = 17.63, p<0.0001	0.06	N
	other b/t wet and dry seasons in adult females	(1, *N*=10595) = 14.07, p=0.0002	0.06	N
6.3.2.5.	inactivity b/t males and females in the dry season	(1, *N*=10619) = 30.63, p<0.0001	0.08	N
	feeding b/t males and females in the dry season	(1, *N*=10619) = 32.19, p<0.0001	0.08	N
	moving b/t males and females in the dry season	(1, *N*=10619) = 64.58, p<0.0001	0.11	N
	socializing b/t males and females in the dry season	(1, *N*=10619) = 355.31, p<0.0001	0.25	Significant
	other b/t males and females in the dry season	(1, *N*=10619) = 19.37, p<0.0001	0.06	N
	feeding b/t males and females in the wet season	(1, *N*=14871) = 73.54, p<0.0001	0.10	N
	moving b/t males and females in the wet season	(1, *N*=14871) = 96.85, p<0.0001	0.11	N
	socializing b/t males and females in the wet season	(1, *N*=14871) = 345.62, p<0.0001	0.21	N

6.3.2.6.	vigilance b/t adults and young in wet season	(1, *N*=5724) = 108.56, p<0.0001	0.19	N
	vigilance b/t males and females in wet season	(1, *N*=4934) = 263.1, p<0.0001	0.32	Significant
	vigilance b/t males and females in dry season	(1, *N*=4025) = 77.99, p<0.0001	0.19	N
6.3.2.7.	travel b/t wet and dry season in all individuals	(1, *N*=8717) = 28.55, p<0.0001	0.08	N
	travel b/t wet and dry season in adults	(1, *N*=7177) = 34.65, p<0.0001	0.10	N
	travel b/t wet and dry season in young	(1, *N*=925) = 15.01, p=0.0001	0.18	N
	travel b/t wet and dry season in adult males	(1, *N*=3746) = 11.38, p=0.0007	0.08	N
	travel b/t wet and dry season in adult females	(1, *N*=3431) = 24.66, p<0.0001	0.12	N
	travel b/t adults and young in the wet season	(1, *N*=3269) = 16.63, p<0.0001	0.10	N
	travel b/t adults and young in the dry season	(1, *N*=4833) = 15.43, p<0.0001	0.08	N
6.3.2.8.	playing b/t wet and dry season in all individuals	(1, *N*=6612) = 20.62, p<0.0001	0.08	N
	grooming b/t wet and dry season in all individuals	(1, *N*=6612) = 62.7, p<0.0001	0.14	N
	vocalizing b/t wet and dry season in all individuals	(1, *N*=6612) = 48.59, p<0.0001	0.12	N
	playing b/t wet and dry season in adults	(1, *N*=5563) = 4.13, p=0.04	0.04	N
	grooming b/t wet and dry season in adults	(1, *N*=5563) = 39.05, p<0.0001	0.12	N
	vocalizing b/t wet and dry season in adults	(1, *N*=5563) = 20.63, p<0.0001	0.09	N
	grooming b/t wet and dry season in young	(1, *N*=763) = 11.97, p=0.0005	0.18	N
	grooming b/t wet and dry season in adult females	(1, *N*=1454) = 14.22, p<0.0001	0.14	N
	vocalizing b/t wet and dry season in adult females	(1, *N*=1454) = 40.83, p<0.0001	0.23	N
	vocalizing b/t adults and young in the dry season	(1, *N*=2580) = 757.08, p<0.0001	0.67	Significant

	playing b/t adults and young in the dry season	(1, *N*=2580) = 1428.7, p<0.0001	0.84	Significant
	grooming b/t adults and young in the dry season	(1, *N*=2580) = 11.99, p=0.0005	0.10	N
	grooming b/t adult males and females in dry season	(1, *N*=2369) = 13.21, p=0.0003	0.11	N
	displaying b/t adult males and females in dry season	(1, *N*=2369) = 11.13, p=0.0008	0.10	N
	vocalizing b/t adults and young in the wet season	(1, *N*=3746) = 1056.29, p<0.0001	0.66	Significant
	displaying b/t adults and young in the wet season	(1, *N*=3746) = 15.71, p<0.0001	0.09	N
	playing b/t adults and young in the wet season	(1, *N*=3746) = 1683.18, p<0.0001	0.79	Significant
	grooming b/t adults and young in the wet season	(1, *N*=3746) = 80.64, p<0.0001	0.21	N
	vocalizing b/t adult males and females in wet season	(1, *N*=3193) = 60.76, p<0.0001	0.19	N
	displaying b/t adult males and females in wet season	(1, *N*=3193) = 14.59, p<0.0001	0.10	N
	playing b/t adult males and females in wet season	(1, *N*=3193) = 19.44, p<0.0001	0.11	N
	grooming b/t adult males and females in wet season	(1, *N*=3193) = 242.24, p<0.0001	0.38	Significant

6.3.3. Monthly activity budgets

6.3.3.1. All individuals

Monthly trends in activity budget categories for all individuals are shown in Figure 6.19 and Table 6.6.

Moving was significantly and positively correlated to temperature (r (16) = 0.55, p = 0.03) (Figure 6.20), and significantly and negatively correlated to flowering (r (13) = -0.71, p = 0.007) (Figure 6.21). This indicates doucs moved more when it was warmer and less when flowers were most abundant.

Social activity, inactivity, feeding and self-grooming were not significantly correlated to weather variables, phenology, variation in the use of home range, or the degree of unit cohesion. Feeding was not significantly correlated to fruiting or flowering (Figure 6.22).

Figure 6.19. Monthly variation in the activity budget in all individuals.

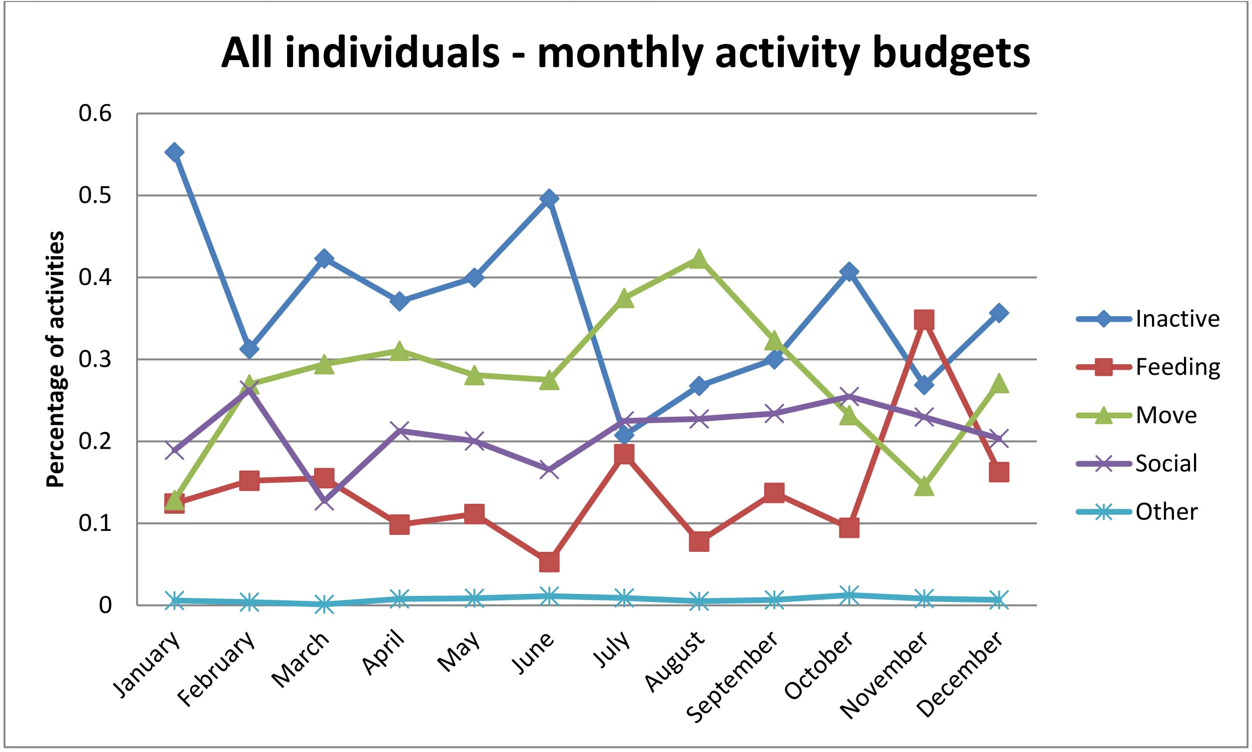


Table 6.6. Monthly activity budget in all individuals (dry season=February through May).

		Inactive	Feeding	Moving	Social	Other	Total N
January	%	55.2	12.4	12.9	18.9	0.6	677
	N-value	374	84	87	128	4	
February	%	31.3	15.2	26.9	26.2	0.4	4758
	N-value	1487	723	1281	1249	18	
March	%	42.3	15.5	29.4	12.7	0.1	2835
	N-value	1199	439	833	361	3	
April	%	27.1	9.8	31.0	21.3	0.8	1659
	N-value	615	163	515	353	13	
May	%	40.0	11.1	28.1	20.0	0.8	3552
	N-value	1419	395	997	711	30	
June	%	49.6	5.3	27.5	16.5	1.1	1801
	N-value	893	95	495	298	20	
July	%	20.7	18.4	37.5	22.5	0.9	787
	N-value	163	145	295	177	7	
August	%	26.7	7.8	42.3	22.7	0.5	3704

	N-value	990	288	1566	842	18	
September	%	30.0	13.7	32.3	23.4	0.6	3012
	N-value	903	412	974	704	19	
October	%	40.7	9.5	23.2	25.4	1.2	3381
	N-value	1376	319	784	860	42	
November	%	26.8	34.9	14.5	23.0	0.8	2138
	N-value	574	745	311	491	17	
December	%	35.6	16.2	27.1	20.4	0.7	2137
	N-value	762	347	579	435	14	
Total N		10755	4155	8717	6609	205	30441

Figure 6.20. Monthly variation in moving and temperature (dry season=February through May).

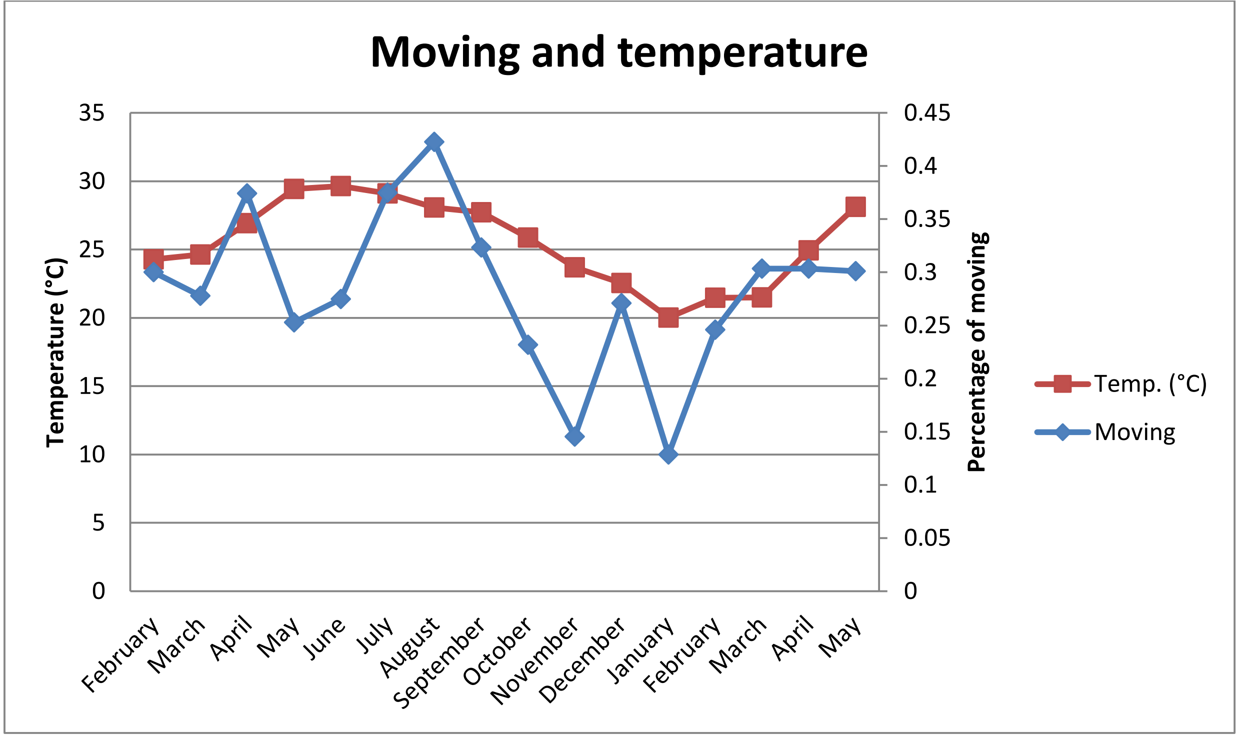


Figure 6.21. Monthly variation in moving and flowering (dry season=February through May).

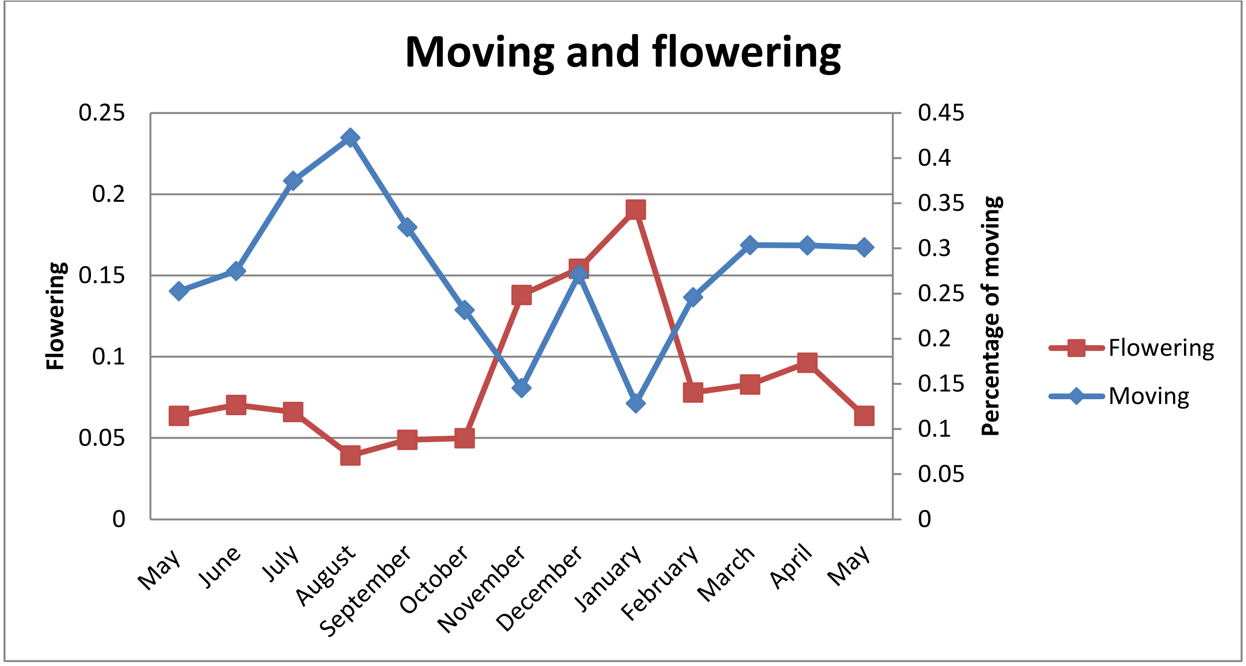
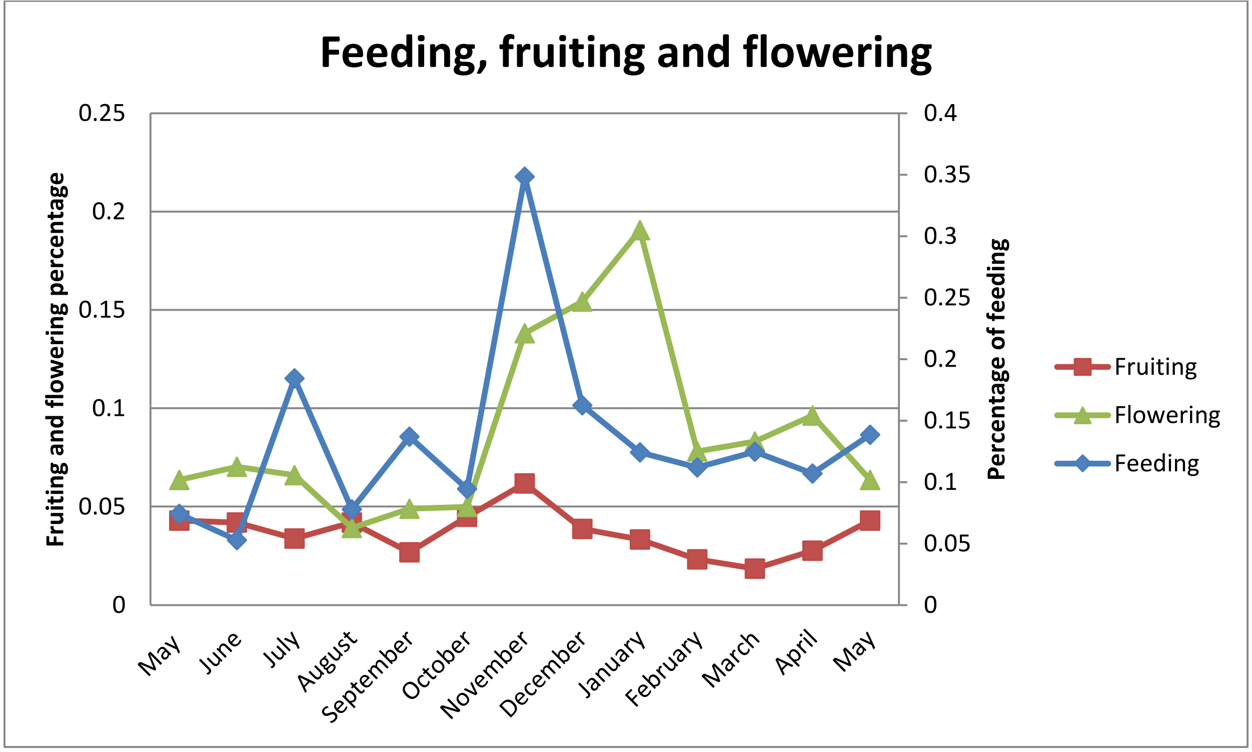


Figure 6.22. Monthly variation in feeding, fruiting and flowering.



6.3.3.2. Adults and young individuals

Monthly activity budgets of adults are shown in Figure 6.23 and Table 6.7. Self-grooming was significantly and positively correlated to temperature (r (16) = 0.51, p = 0.04), indicating it is more frequent when it is warmer. Moving remained significantly and positively correlated to temperature (r (16) = 0.53, p = 0.03), and significantly and negatively correlated to flowering (r (13) = -0.65, p = 0.02), indicating adults moved more when it was warmer, and moved less when flowers were abundant.

Inactivity, social behaviors, and feeding were not significantly correlated to weather variables, phenology variables, variation in the use of home range, or unit cohesion.

Monthly activity budgets in young individuals are shown in Figure 6.24 and Table 6.8. At this scale of analysis my sample size for young individuals is insufficient and it is not possible to identify monthly trends. For example, July and January show a significant increase in social behaviors in young individuals (Figure 6.24), but these months contain only 14 and 32 total observations on “young” individuals of which most are social observations (Table 6.8). In July there were no observations of young individuals as inactive, suggesting 0% inactivity. Of course this fails to accurately reflect activity budgets. Considering these concerns, no analyses are presented.

6.23. Monthly variation in adult activity budgets (dry season=February through May).

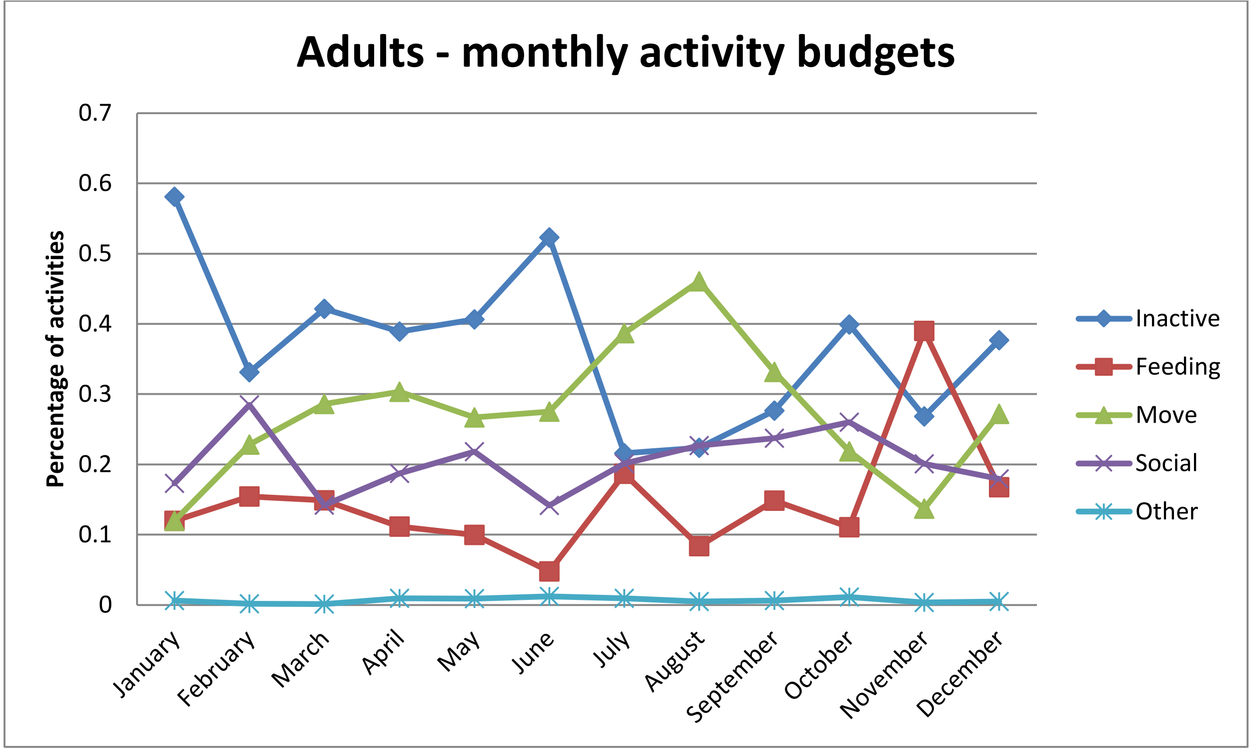


Table 6.7. Monthly activity budget in adults (dry season=February through May).

		Inactive	Feeding	Moving	Social	Other	Total N
January	%	58.1	12.0	12.0	17.3	0.6	642
	N-value	373	77	77	111	4	
February	%	33.1	15.4	22.8	28.5	0.2	3977
	N-value	1317	614	908	1132	6	
March	%	42.1	14.9	28.6	14.2	0.2	2222
	N-value	936	331	636	316	3	
April	%	38.9	11.1	30.4	18.7	0.9	1401
	N-value	545	156	425	262	13	
May	%	40.6	10.0	26.7	21.8	0.9	3018
	N-value	1227	301	805	658	27	
June	%	52.3	4.8	27.5	14.2	1.2	1315
	N-value	688	63	362	186	16	
July	%	21.6	18.7	38.7	20.1	0.9	755
	N-value	163	141	292	152	7	
August	%	22.4	8.4	46.0	22.7	0.5	3132
	N-value	701	262	1443	711	15	
September	%	27.6	14.9	33.2	23.7	0.6	2646
	N-value	731	393	878	628	16	
October	%	39.9	11.1	21.9	26.0	1.1	2743
	N-value	1095	303	600	714	31	
November	%	26.8	39.1	13.7	20.1	0.3	1751

	N-value	470	683	240	352	6	
December	%	37.6	16.8	27.2	17.9	0.5	1880
	N-value	708	315	511	337	9	
Total N		8954	3639	7177	5559	153	25482

Figure 6.24. Monthly variation in young individuals activity budget.

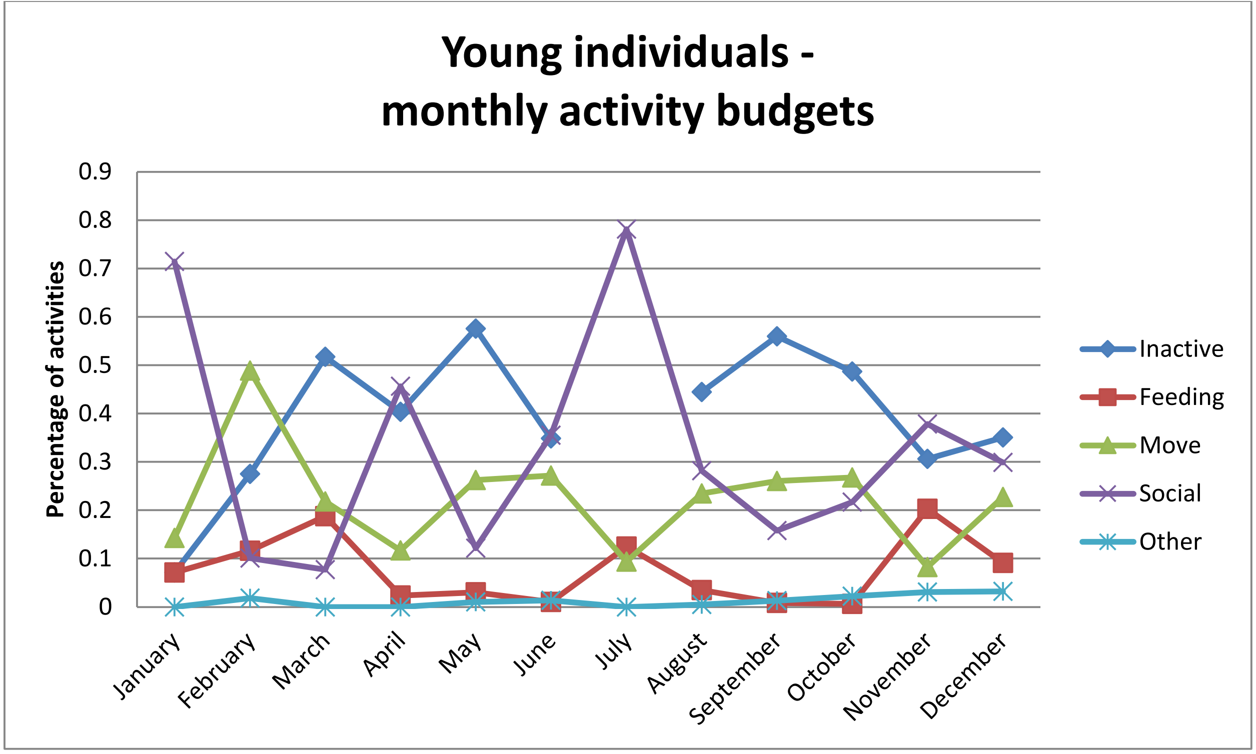


Table 6.8. Monthly activity budget in young individuals (dry season=February through May).

		Inactive	Feeding	Moving	Social	Other	Total N
January	%	7.1	7.2	14.3	71.4	0	14
	N-value	1	1	2	10	0	
February	%	27.5	11.6	48.9	10.1	1.9	593
	N-value	163	69	290	60	11	
March	%	51.7	18.8	21.8	7.8	0	491
	N-value	254	92	107	38	0	
April	%	40.4	2.3	11.7	45.6	0	171
	N-value	69	4	20	78	0	
May	%	57.6	3.0	26.3	12.1	1.0	297
	N-value	171	9	78	36	3	
June	%	34.8	1.1	27.2	35.5	1.4	287
	N-value	100	3	78	102	4	
July	%	0	12.5	9.4	78.1	0	32
	N-value	0	4	3	25	0	
August	%	44.4	3.5	23.4	28.2	0.5	405
	N-value	180	14	95	114	2	

September	%	56.0	0.8	26.1	15.8	1.3	234
	N-value	131	2	61	37	3	
October	%	48.7	0.6	26.8	21.7	2.2	493
	N-value	240	3	132	107	11	
November	%	30.6	20.3	8.2	37.8	3.1	291
	N-value	89	59	24	110	9	
December	%	35.1	9.1	22.7	29.9	3.2	154
	N-value	54	14	35	46	5	
Total N		1452	274	925	763	48	3462

6.3.3.3. Adult males and adult females

Monthly activity budgets of adult males and adult females are shown in Figures 6.25 and 6.26, and Table 6.9 and 6.10.

In adult males, self-grooming was significantly and positively correlated to temperature (r (16) = 0.48, p = 0.05), indicating it was more common when it was warmer. In adult females, self-grooming was significantly and positively correlated with precipitation (r (16) = 0.51, p = 0.04), indicating it was more common with increases in rainfall.

In adult females, moving remained significantly and positively correlated to temperature (r (16) = 0.57, p = 0.02). This correlation was non-significant but moderate in adult males (r (16) = 0.46, p = 0.07). For both adult males and adult females moving remained significantly and negatively correlated to flowering (males, r (16) = -0.59, p = 0.03, and females, r (16) = -0.67, p = 0.01). These results indicate adults moved more when it was warmer, and moved less when flowers were abundant.

In both adult males and adult females, inactivity, social behaviors, and feeding were not significantly correlated to weather variables, phenology variables, variation in the use of home range, or unit cohesion.

Figure 6.25. Monthly variation in adult males activity budget.

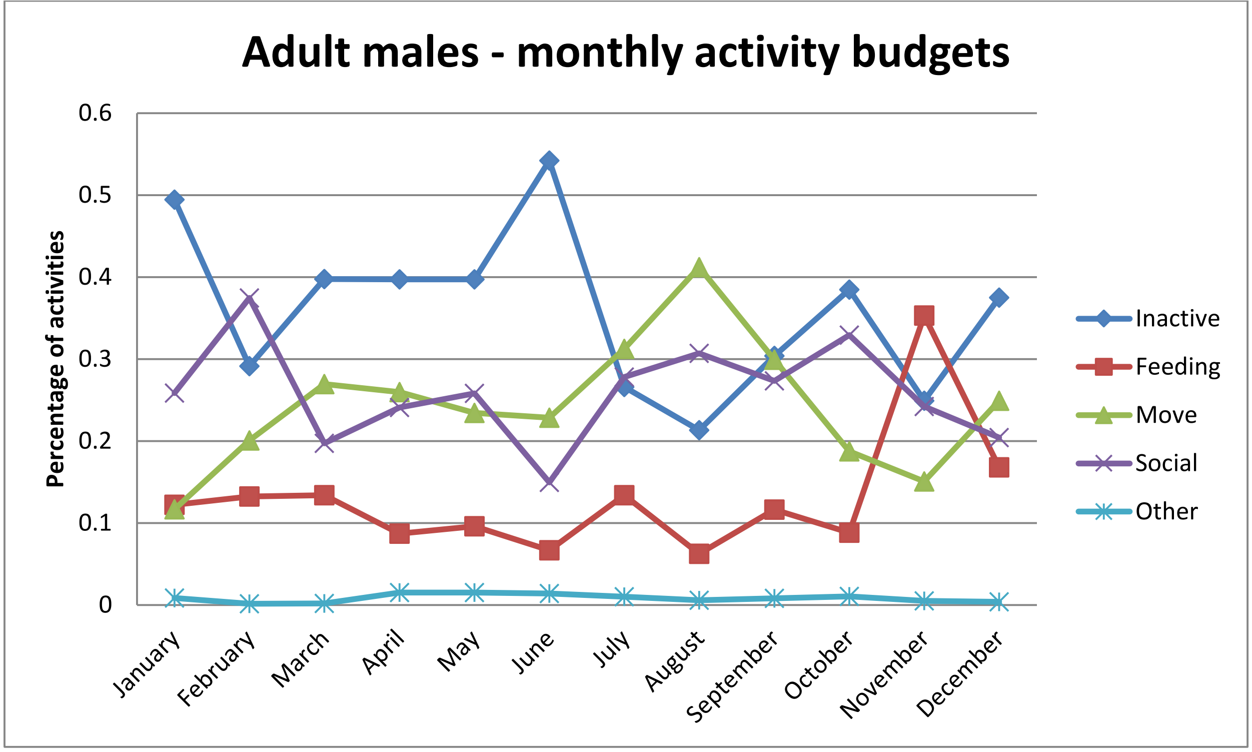


Figure 6.26. Monthly variation in adult females activity budget.

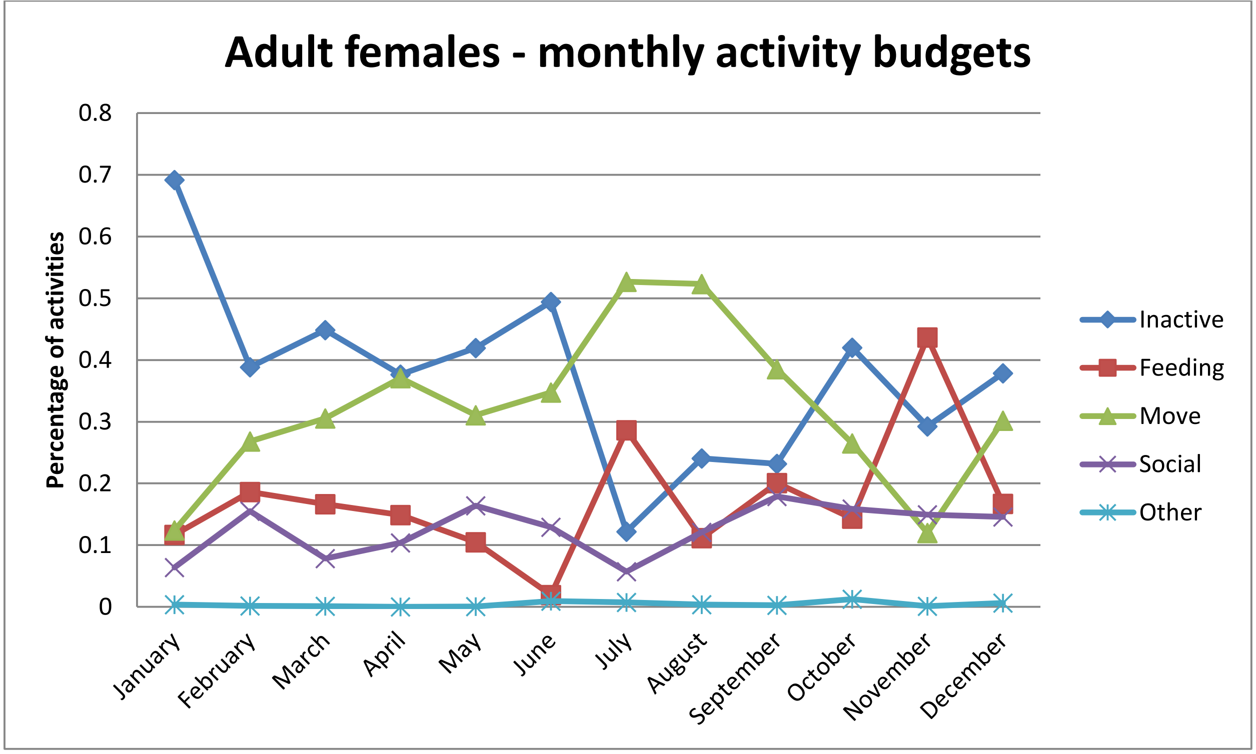


Table 6.9. Monthly activity budget in adult males (dry season=February through May).

		Inactive	Feeding	Moving	Social	Other	Total N
January	%	49.5	12.2	11.7	25.8	0.8	360
	N-value	178	44	42	93	3	
February	%	29.2	13.2	20.1	37.4	0.1	2351
	N-value	685	311	472	880	3	
March	%	39.8	13.4	26.9	19.7	0.2	1202
	N-value	478	161	324	237	2	
April	%	39.7	8.7	26.0	24.1	1.5	851
	N-value	338	74	221	205	13	
May	%	39.7	9.6	23.4	25.8	1.5	1733
	N-value	688	166	406	447	26	
June	%	54.2	6.7	22.8	14.9	1.4	797
	N-value	432	53	182	119	11	
July	%	26.6	13.4	31.2	27.8	1.0	493
	N-value	131	66	154	137	5	
August	%	21.3	6.2	41.2	30.7	0.6	1782
	N-value	380	111	734	547	10	
September	%	30.4	11.6	29.9	27.3	0.8	1636
	N-value	497	190	489	447	13	
October	%	38.5	8.8	18.8	32.9	1.0	1643
	N-value	632	145	308	541	17	
November	%	24.9	35.3	15.1	24.2	0.5	975
	N-value	243	344	147	236	5	
December	%	37.5	16.8	24.9	20.4	0.4	1072
	N-value	402	180	267	219	4	
Total N		5084	1845	3746	4108	112	14895

Table 6.10. Monthly activity budget in adult females (dry season=February through May).

		Inactive	Feeding	Moving	Social	Other	Total N
January	%	69.1	11.7	12.4	6.4	0.4	282
	N-value	195	33	35	18	1	
February	%	38.9	18.6	26.8	15.5	0.2	1626
	N-value	632	303	436	252	3	
March	%	44.9	16.6	30.6	7.8	0.1	1021
	N-value	458	170	312	80	1	
April	%	37.6	14.9	37.1	10.4	0.0	550
	N-value	207	82	204	57	0	
May	%	41.9	10.5	31.1	16.4	0.1	1285
	N-value	539	135	399	211	1	
June	%	49.4	1.9	34.8	12.9	1.0	518
	N-value	256	10	180	67	5	
July	%	12.2	28.6	52.7	5.7	0.8	262
	N-value	32	75	138	15	2	
August	%	24.1	11.1	52.3	12.1	0.4	1355

	N-value	326	151	709	164	5	
September	%	23.2	20.1	38.5	17.9	0.3	1010
	N-value	234	203	389	181	3	
October	%	42.0	14.3	26.5	15.9	1.3	1102
	N-value	463	158	292	175	14	
November	%	29.2	43.7	12.0	15.0	0.1	776
	N-value	227	339	93	116	1	
December	%	37.9	16.7	30.2	14.6	0.6	808
	N-value	306	135	244	118	5	
Total N		3875	1794	3431	1454	41	10595

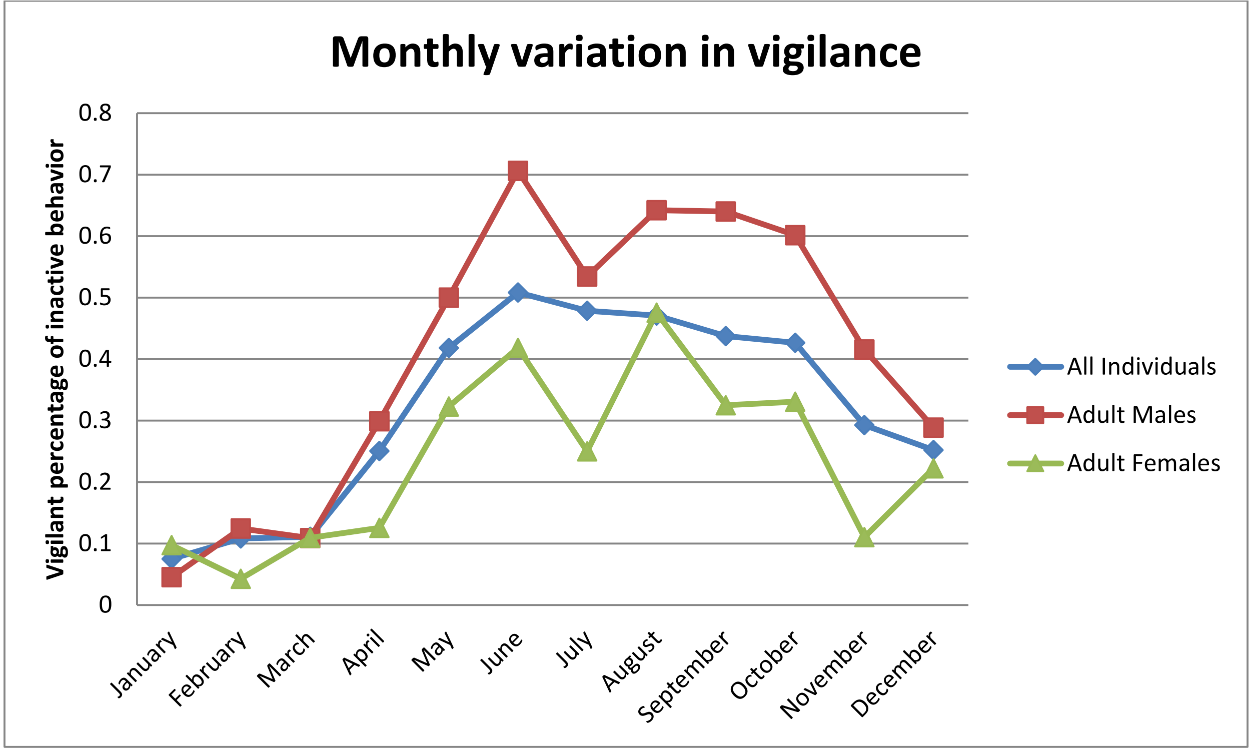
6.3.3.4. Monthly "inactive" subcategory behaviors

Figure 6.27 shows the monthly variation of vigilant behaviors in all individuals, adult males and adult females. The inverse represents resting.

Vigilance was significantly and positively correlated with temperature and significantly and negatively correlated with flower abundance, indicating vigilance increased in warmer temperatures, vigilance decreased with flower availability, and resting increased in cooler temperatures: all individuals – temperature (r (16) = 0.66, p = 0.005), flowering (13) = -0.68, p = 0.01); adult males – temperature (r (16) = 0.73, p = 0.001), flowering (r (13) = -0.64, p = 0.02); adult females – temperature (r (16) = 0.55, p = 0.03), flowering (r (13) = -0.61, p = 0.03).

Considering that vigilance increases between May and October, banding may be an additional influence, as this is a time of increased super-trooping, all-male unit formation, increased interspecific associations during parts of these months.

Figure 6.27. Monthly variation in vigilance (dry season=February through May).

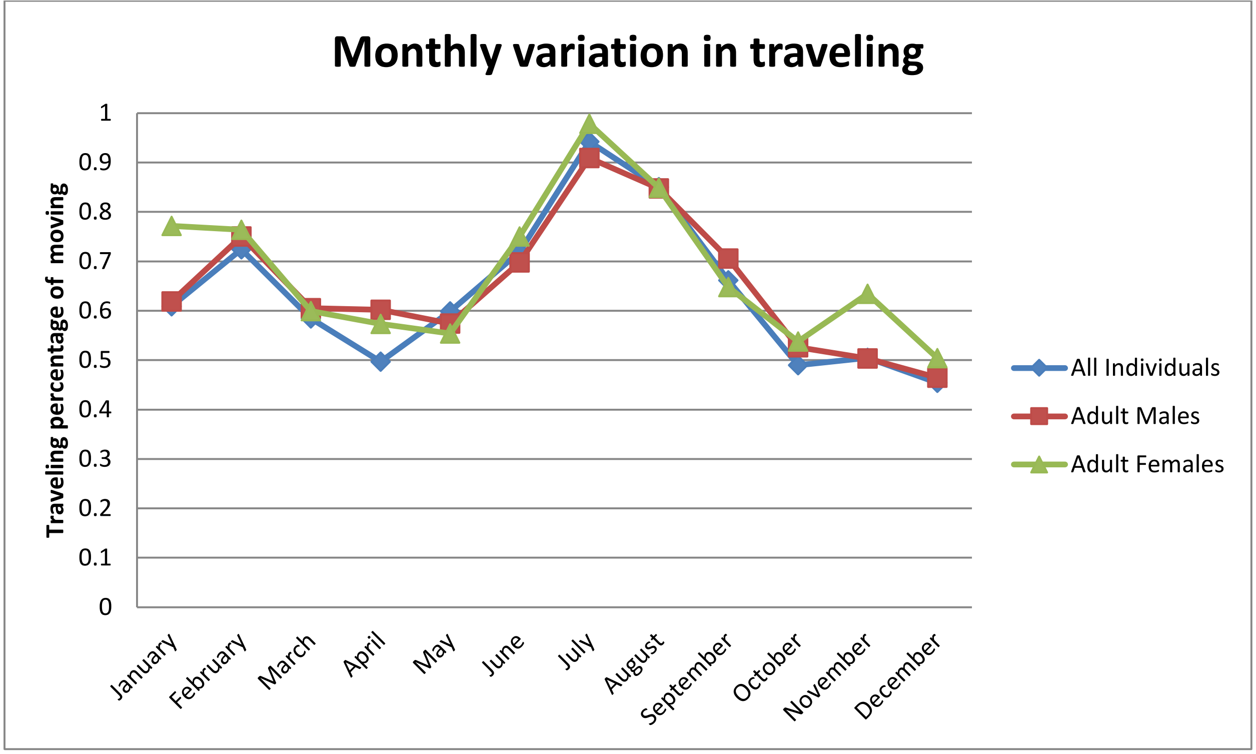


6.3.3.5. Monthly "moving" subcategory behaviors

Figure 6.28 shows the monthly variation of traveling in all individuals, adult males and adult females. The inverse represents local movements.

Traveling was significantly and positively correlated to variations in the use of home range: all individuals (r (12) = 0.72, p = 0.007), adult males (r (12) = 0.72, p = 0.007), adult females (r (12) = 0.58, p = 0.05). This is a common sense conclusion, although it illustrates the applicability of the data. All other correlations were non-significant.

Figure 6.28. Monthly variation in traveling (dry season=February through May).



6.3.3.6. Monthly "social" subcategory behaviors

Figure 6.29 through 6.32 show monthly variation of displaying, vocalizing, playing, and allogrooming in each grouping of individuals. Young individuals are included because there was a larger sample size of social behaviors observed.

Displaying (Figure 6.29) in all individuals, all adults, and adult males was significantly and positively correlated with leaf flush, indicating displaying increased when young leaves were abundant: all individuals (r (13) = 0.68, p = 0.01), adults (r (13) = 0.66, p = 0.01), adult males (r (13) = 0.68, p = 0.01). Vocalizing (Figure 6.30) in all individuals, all adults and adult males was significantly and negatively correlated with leaf flush, indicating they decreased when young leaves were abundant: all individuals (r (13) = -0.64, p = 0.02), adults (r (13) = -0.60, p = 0.03), adult males (r (13) = -0.68, p = 0.01). Vocalizing in young individuals was significantly and negatively correlated with temperature, indicating that when it is colder young individuals vocalize more (r (16) = -0.52, p = 0.05). Playing (Figure 6.31) in young individuals was significantly and positively correlated with temperature, indicating they play more when it is warmer (r (16) = 0.63, p = 0.01). Playing was not correlated to any variable in all individuals or adults. Finally, allogrooming (Figure 6.32) in young individuals was significantly and positively correlated with flowering, indicating they allogroomed and are allogroomed more when flowers are abundant (r (13) = 0.63, p = 0.02). Allogrooming was not correlated to any variable in all individuals or adults.

Figure 6.29. Monthly variation in displaying (dry season=February through May).

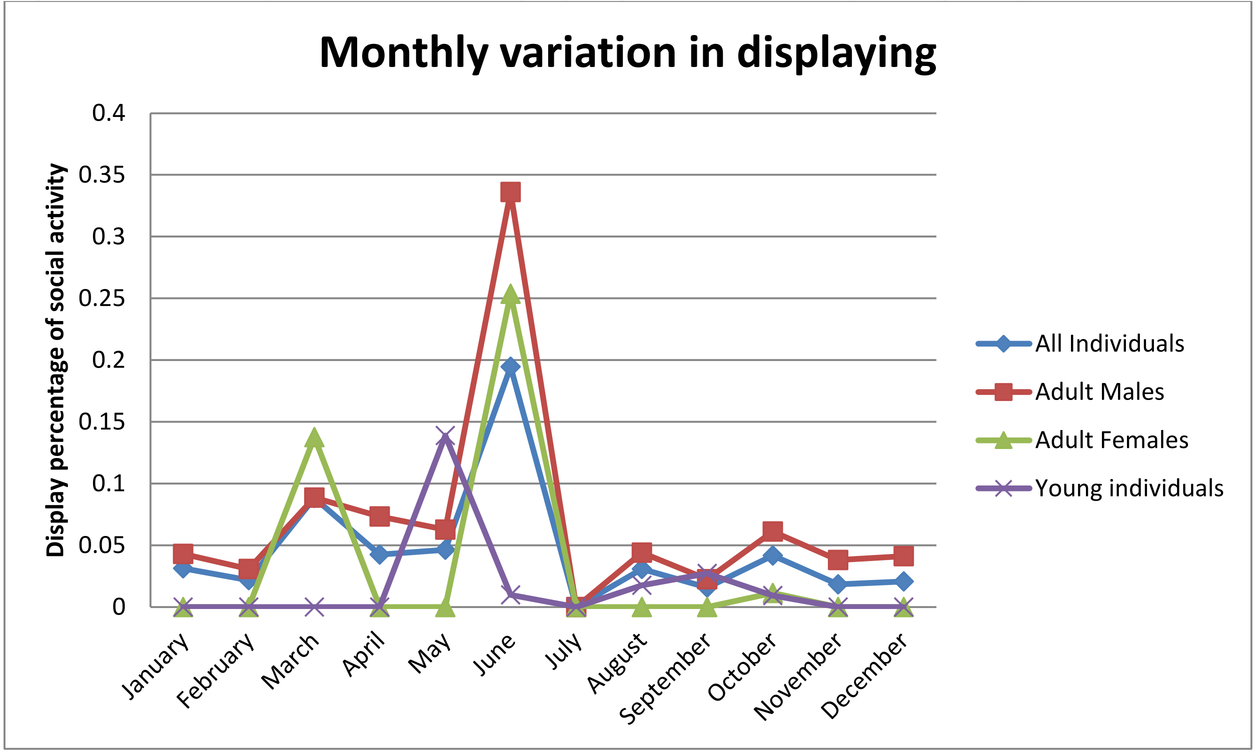


Figure 6.30. Monthly variation in vocalizing (dry season=February through May).

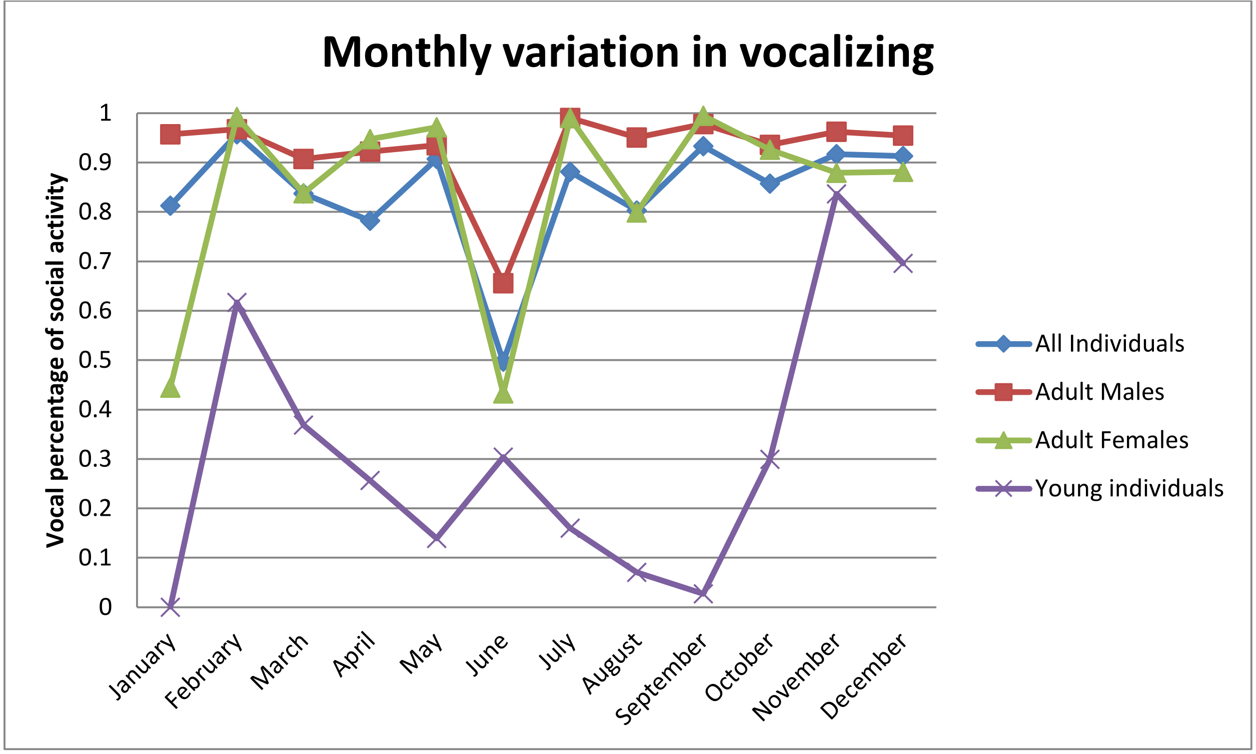


Figure 6.31. Monthly variation in play behavior (dry season=February through May).

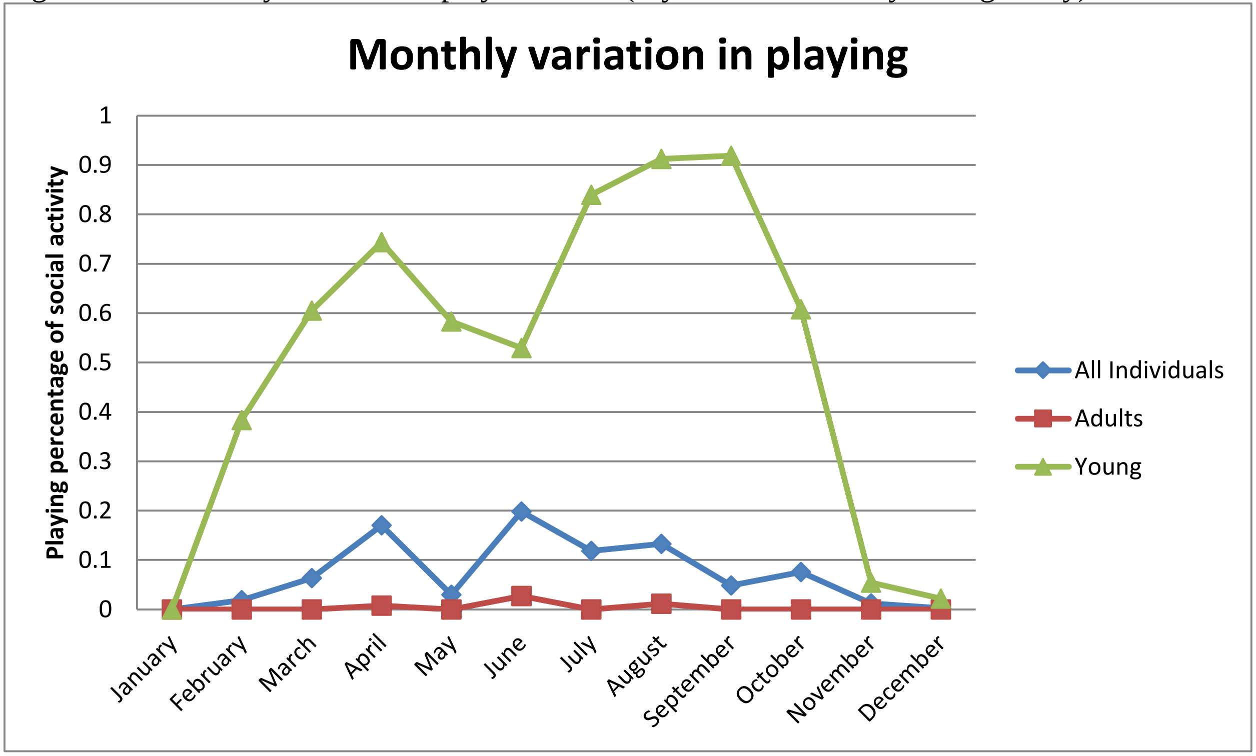
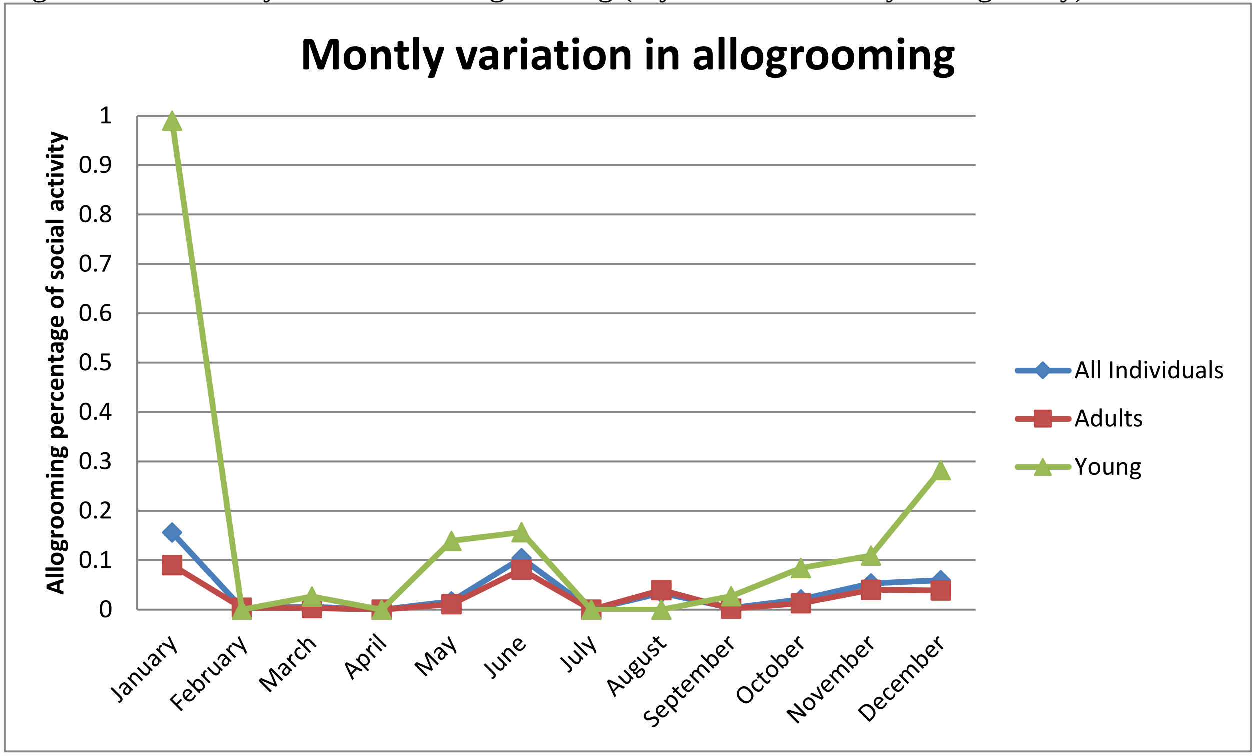


Figure 6.32. Monthly variation in allogrooming (dry season=February through May).



6.3.4. Daily activity budget

6.3.4.1. Annual daily activity budget

Daily activity budgets of all individuals are shown in Figure 6.33 and Table 6.11. The earliest activity aside from sleeping was observed at 5:27 and the latest activity aside from sleeping was observed at 18:18.

There were two peaks in feeding which occurred between 6:00 and 8:00, and between 14:00 and 17:00. There is a minor secondary feeding peak between 12:00 and 13:00. Inactivity generally follows the opposite pattern of feeding, and peaks from 8:00 to 14:00. Moving remains relatively constant throughout the day with minor peaks between 6:00 and 8:00 and 12:00 to 17:00, corresponding to peaks in feeding. Social activity also remains relatively constant throughout the day with the most distinguished peak from 16:00 to 17:00, and two minor peaks corresponding to peaks in inactivity.

This pattern is similar for all adults (Figure 6.34), adult males (Figure 6.35) and adult females (Figure 6.36), but adult males engage in more social behaviors throughout the day than adult females. The daily activity budget among young individuals (Figure 6.37) deviates from this pattern, although feeding and moving peaks are still present. The differences are most likely the result of adult sampling bias and small sample size among young individuals.

Figure 6.33. Daily activity budget in all individuals (annual results).

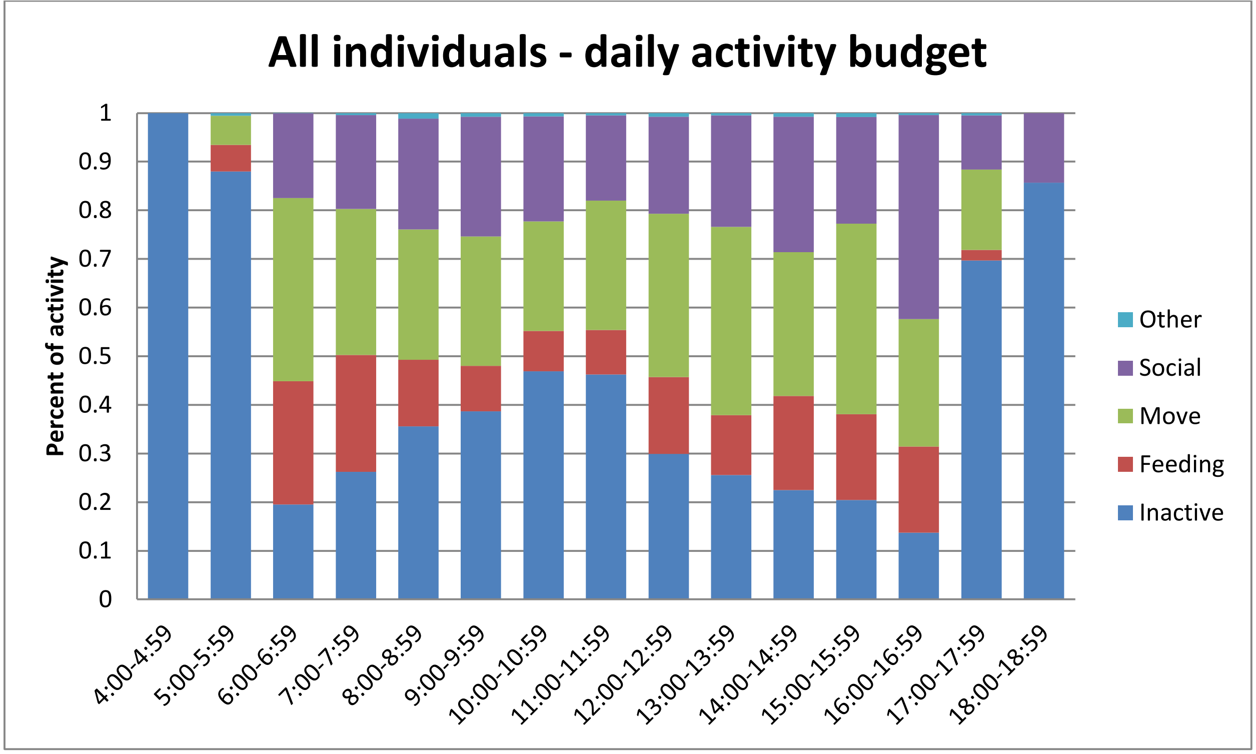


Figure 6.34. Daily activity budget in adults (annual results).

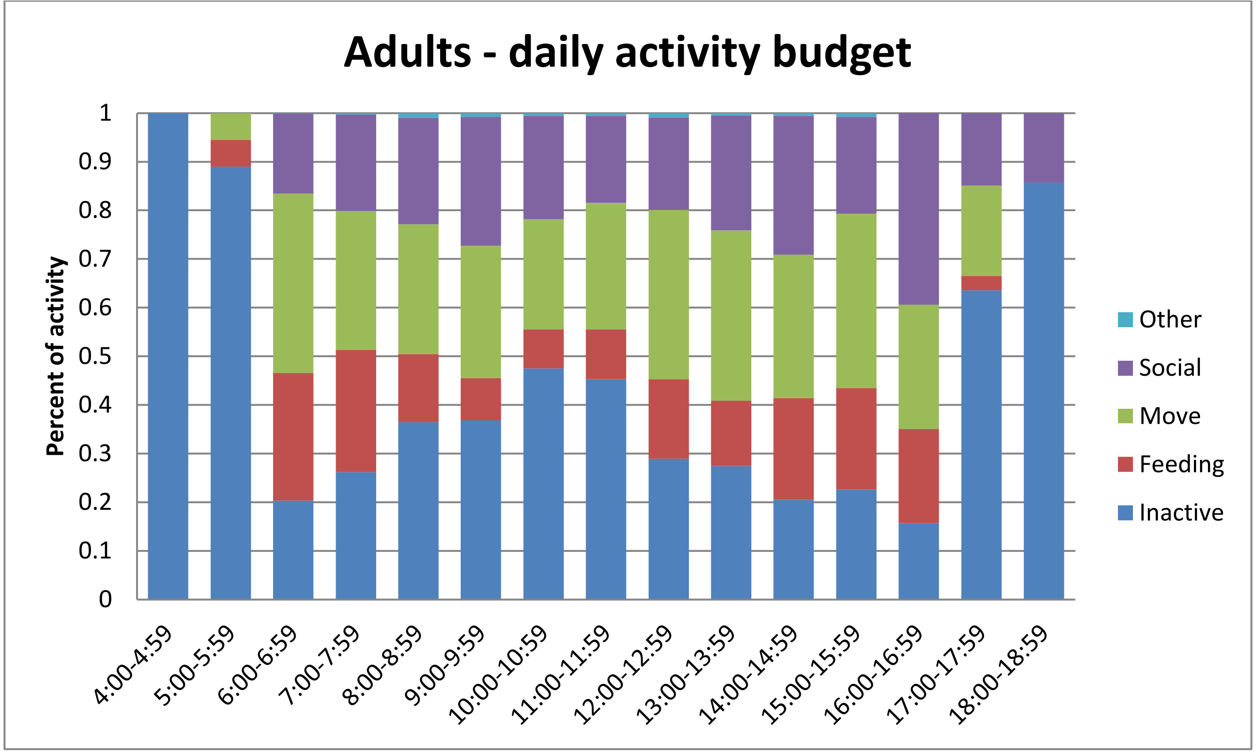


Figure 6.35. Daily activity budget in adult males (annual results).

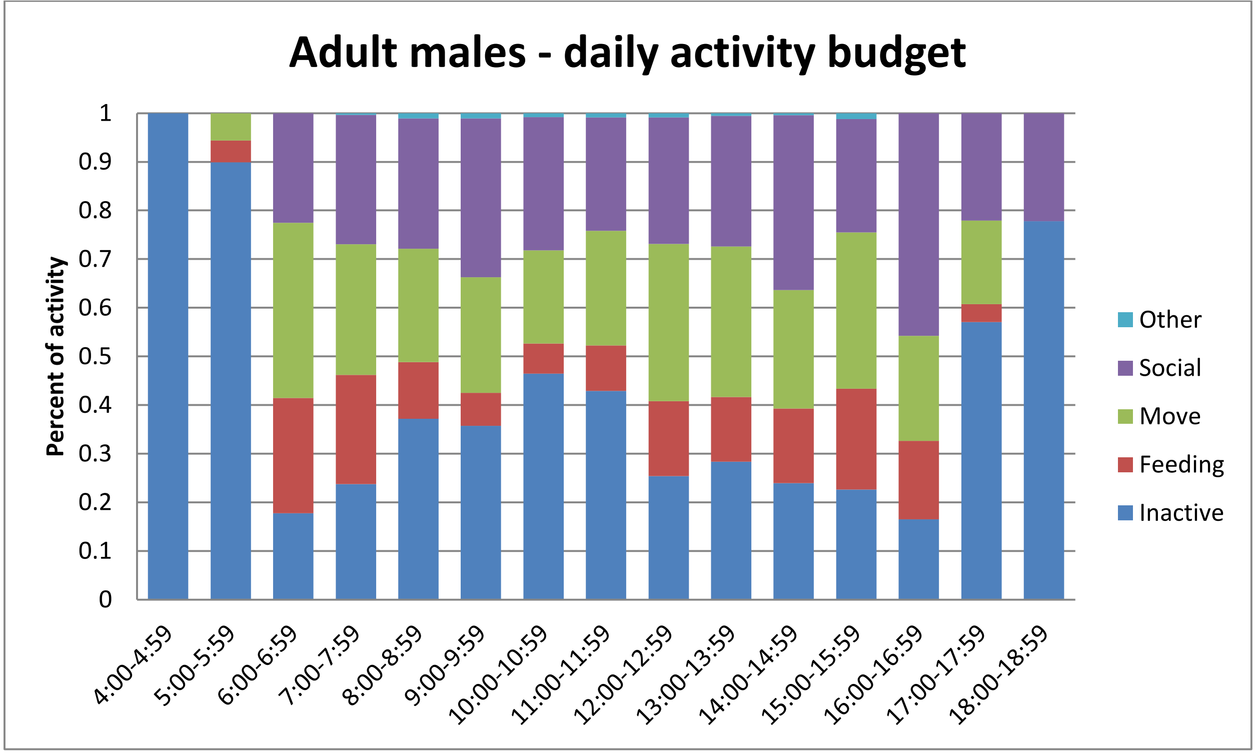


Figure 6.36. Daily activity budget in adult females (annual results).

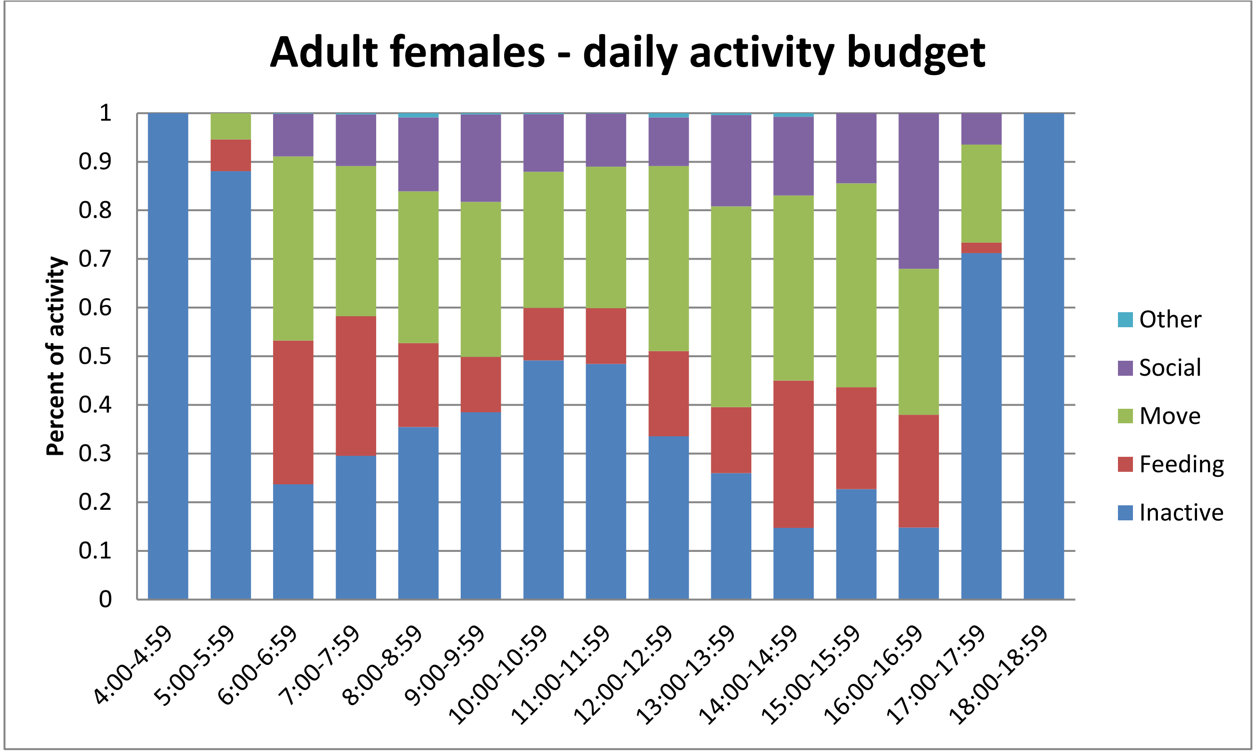


Figure 6.37. Daily activity budget in young individuals (annual results).

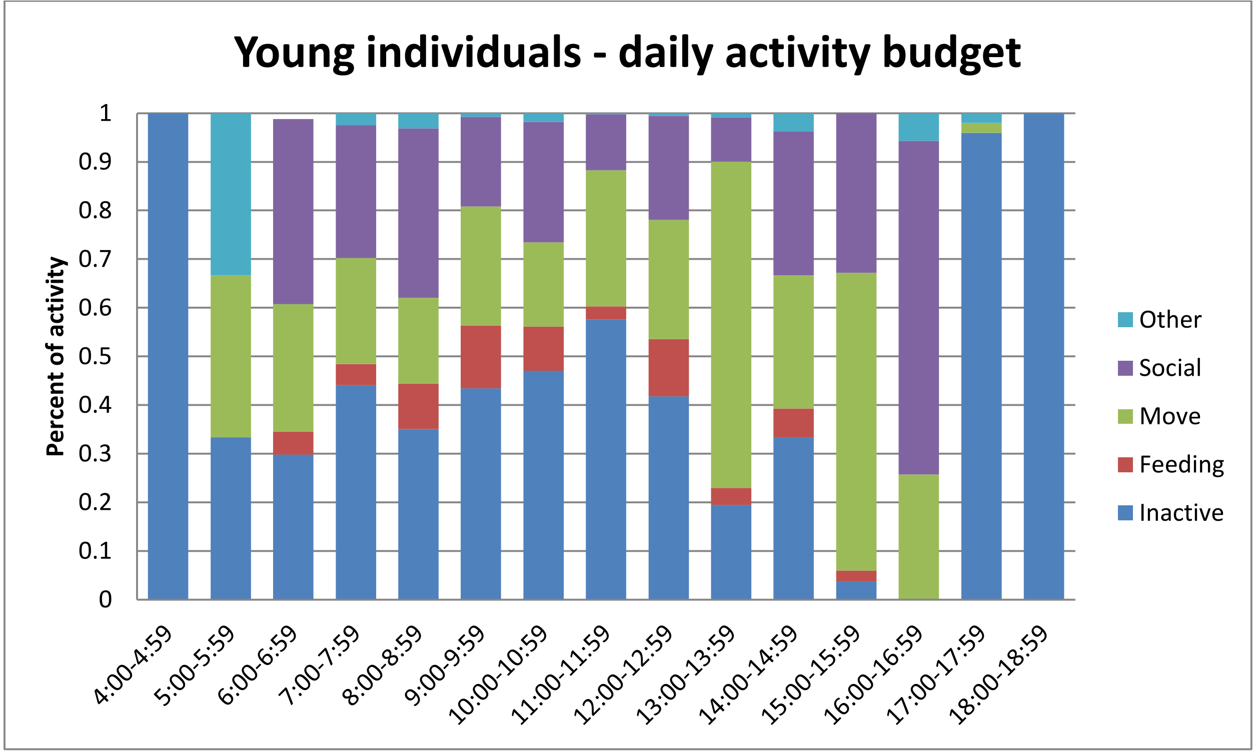


Table 6.11. Hourly activity budget in all individuals.

	Inactive		Feeding		Moving		Social		Other		Total
	%	N	%	N	%	N	%	N	%	N	
4:00-4:59	100.0	60	0.0	0	0.0	0	0.0	0	0.0	0	60
5:00-5:59	88.0	161	5.5	10	6.0	11	0.0	0	0.5	1	183
6:00-6:59	19.5	321	25.3	417	37.7	620	17.4	287	0.1	1	1646
7:00-7:59	26.2	766	24.1	702	30.0	876	19.3	564	0.4	12	2920
8:00-8:59	35.6	1615	13.7	624	26.8	1217	22.8	1036	1.1	51	4543
9:00-9:59	38.6	1961	9.4	475	26.6	1348	24.7	1251	0.7	38	5073
10:00-10:59	46.9	2035	8.3	361	22.5	978	21.6	935	0.7	31	4340
11:00-11:59	46.3	1575	9.1	311	26.6	907	17.5	597	0.5	16	3406
12:00-12:59	29.9	691	15.8	364	33.6	776	19.9	460	0.8	18	2309
13:00-13:59	25.6	556	12.3	268	38.7	843	22.9	498	0.5	11	2176
14:00-14:59	22.5	377	19.3	324	29.6	495	27.8	466	0.8	13	1675
15:00-15:59	20.4	233	17.7	201	39.2	446	21.9	250	0.8	9	1139
16:00-16:59	13.7	69	17.7	89	26.2	132	42.0	211	0.4	2	503
17:00-17:59	69.7	287	2.2	9	16.5	68	11.2	46	0.5	2	412
18:00-18:59	85.7	48	0	0	0	0	14.3	8	0	0	56
Total	10755		4155		8717		6609		205		30441

6.3.4.2. Daily activity budget and unit cohesion

Daily activity budgets of all individuals were compared to the degree of unit cohesion. The percentage of fission represents the percentage of each hour that is spent in a fissioned state, with the percentage of fusion being the inverse. Figures 6.38, 6.39 and 6.40 illustrate the degree of unit cohesion with inactivity, feeding, and moving behaviors. All analyses were significantly correlated: inactivity (r (14) = -0.63, p = 0.01), feeding (r (14) = 0.58, p = 0.03), and moving (r

(14) = 0.69, p = 0.01). This indicates that when units are fused as a group they are significantly more inactive, and when groups are fissioned into units they move and feed significantly more. Thus, groups fission into foraging units daily. Socializing and self-grooming do not correlate to unit cohesion.

Figure 6.41 illustrates the hourly variation in vocalizations and unit cohesion. These form a significant and positive correlation, indicating that vocalizations increase when units are fissioned and decrease when units are fused (r (14) = 0.81, p = 0.0004). This suggests calls may be used to coordinate activities between dispersed foraging units. Figure 6.42 illustrates the hourly variation in vigilance and unit cohesion. These also form a significant and positive correlation, indicating that individuals are more vigilant when units were fissioned and less vigilant when units were fused (r (14) = 0.68, p = 0.01).

Figure 6.38. Inactivity and the degree of unit cohesion in all individuals.

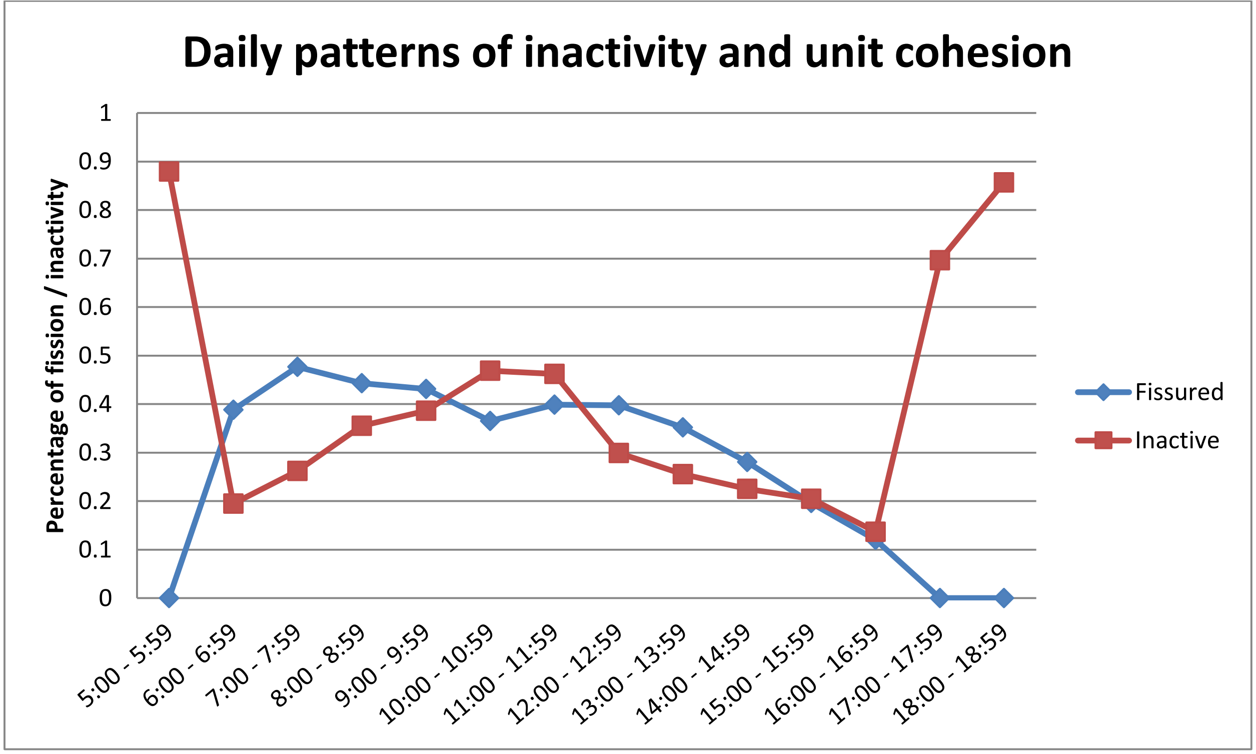


Figure 6.39. Feeding and the degree of unit cohesion in all individuals.

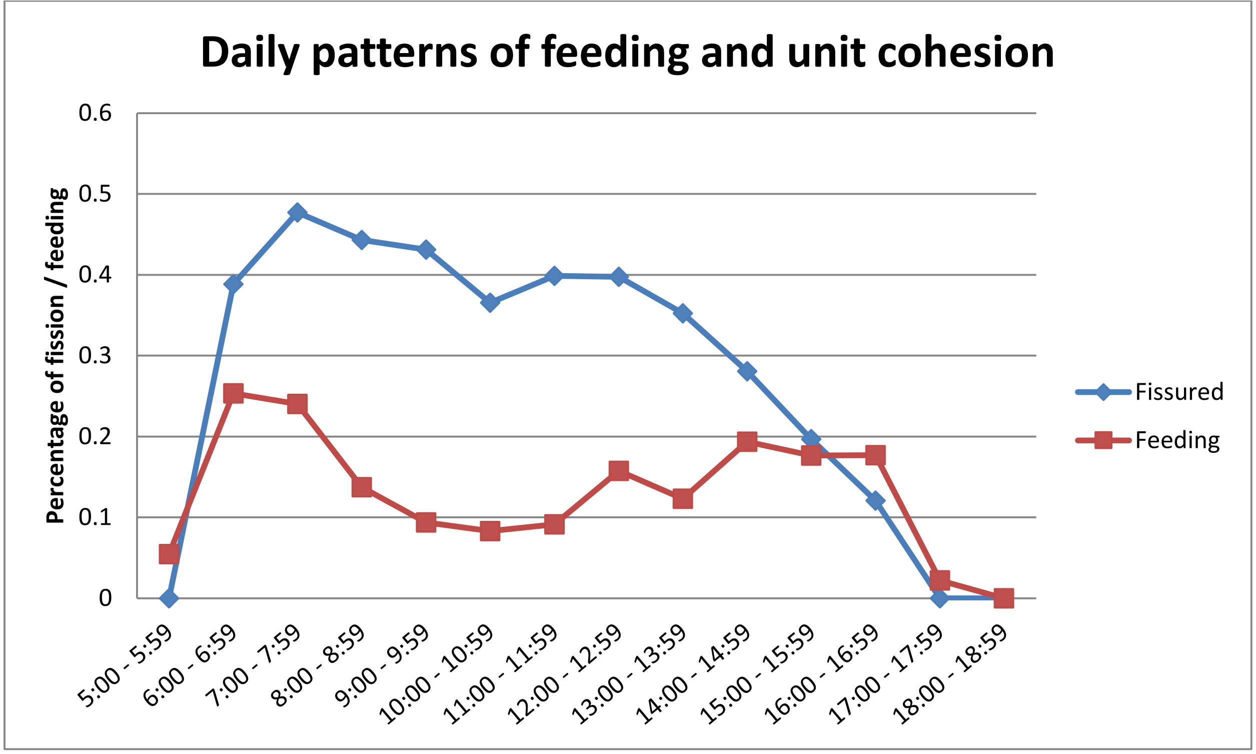


Figure 6.40. Moving and the degree of unit cohesion in all individuals.

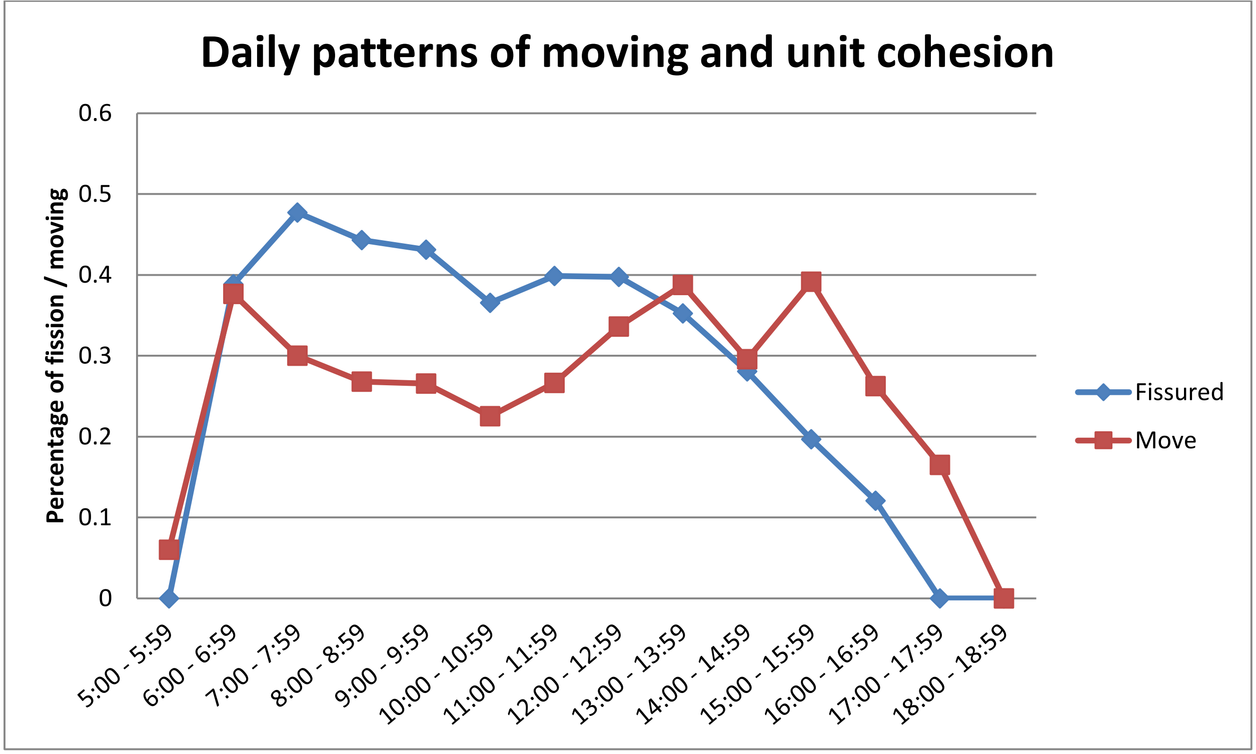


Figure 6.41. Vocalizing and the degree of unit cohesion in all individuals.

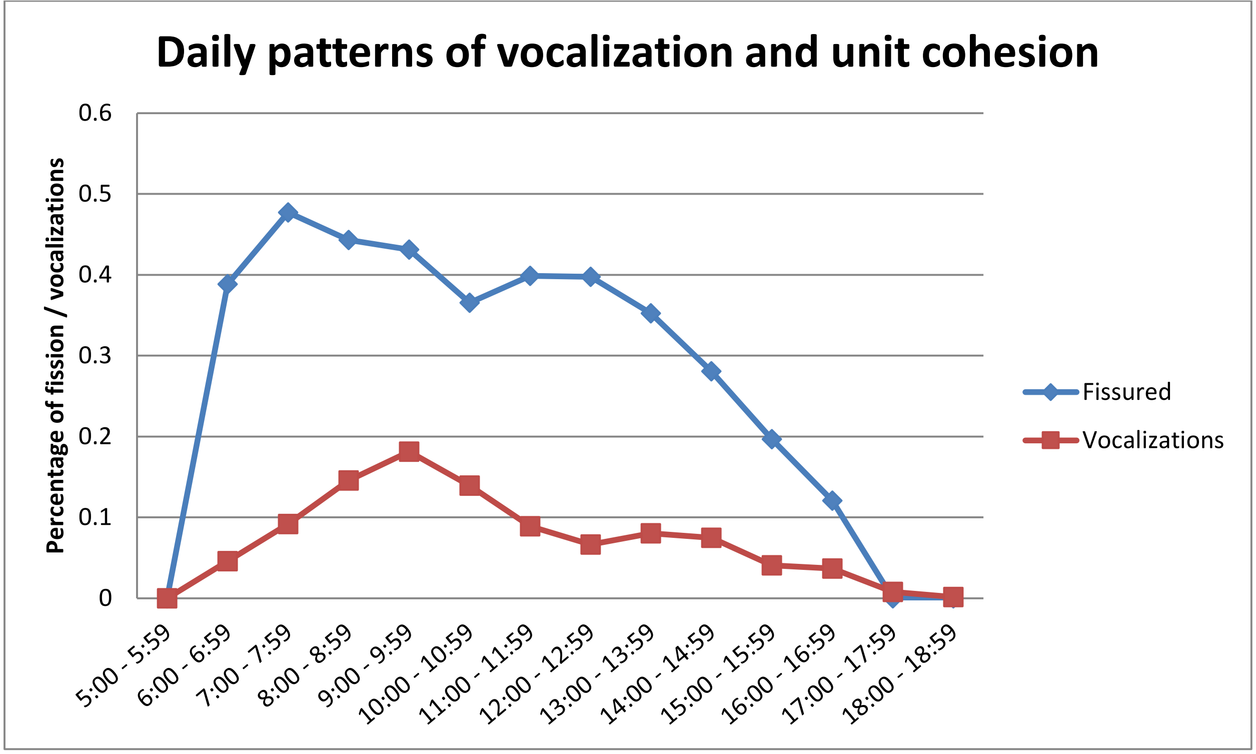
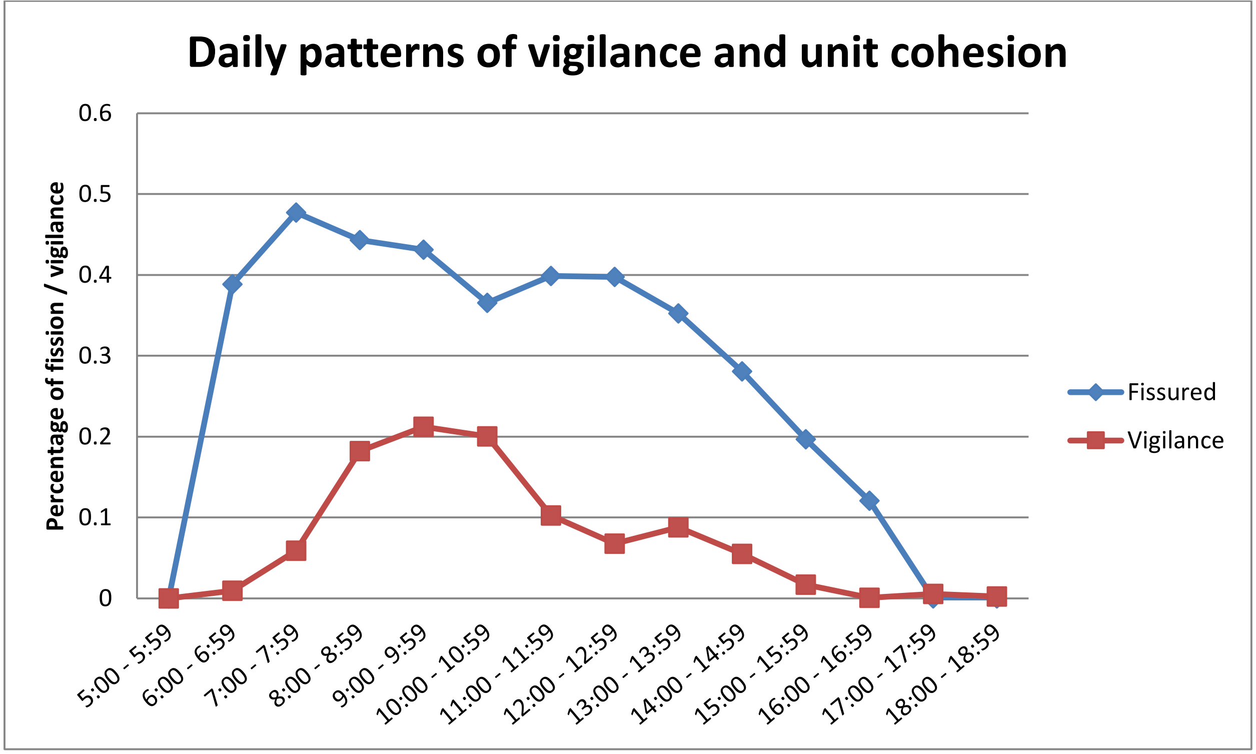


Figure 6.42. Vigilance and the degree of unit cohesion in all individuals.



6.3.4.3. Seasonal daily activity budget

Daily activity budgets of all individuals are compared between the dry season (Figure 6.43) and the wet season (Figure 6.44).

In the dry season, activities other than sleeping began an hour earlier and ended an hour later than in the wet season. There was more social activity during the end of the day during the dry season than during the wet season. Otherwise, all individuals, all adults, adult males, adult females, and young individuals have wet and dry season daily activity budgets which closely resemble their annual daily activity budgets. For this reason only seasonal graphs for all individuals are shown.

Figure 6.43. Dry season daily activity budget in all individuals.

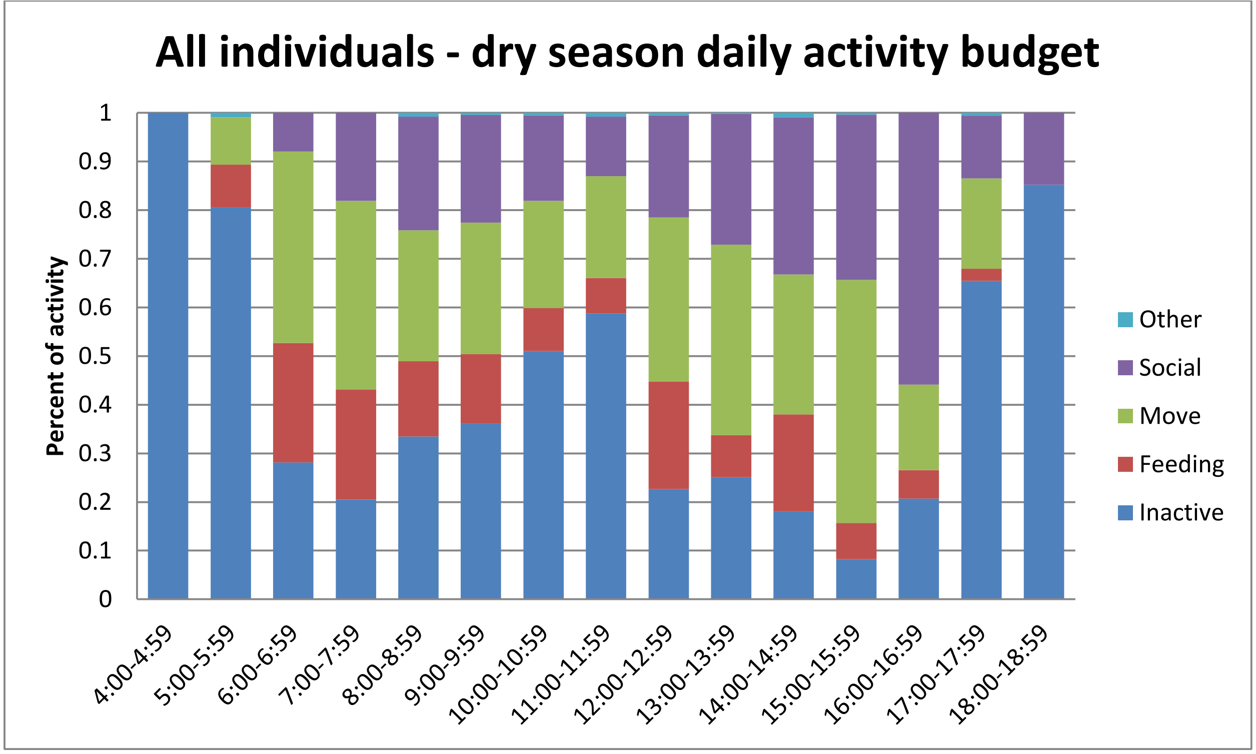
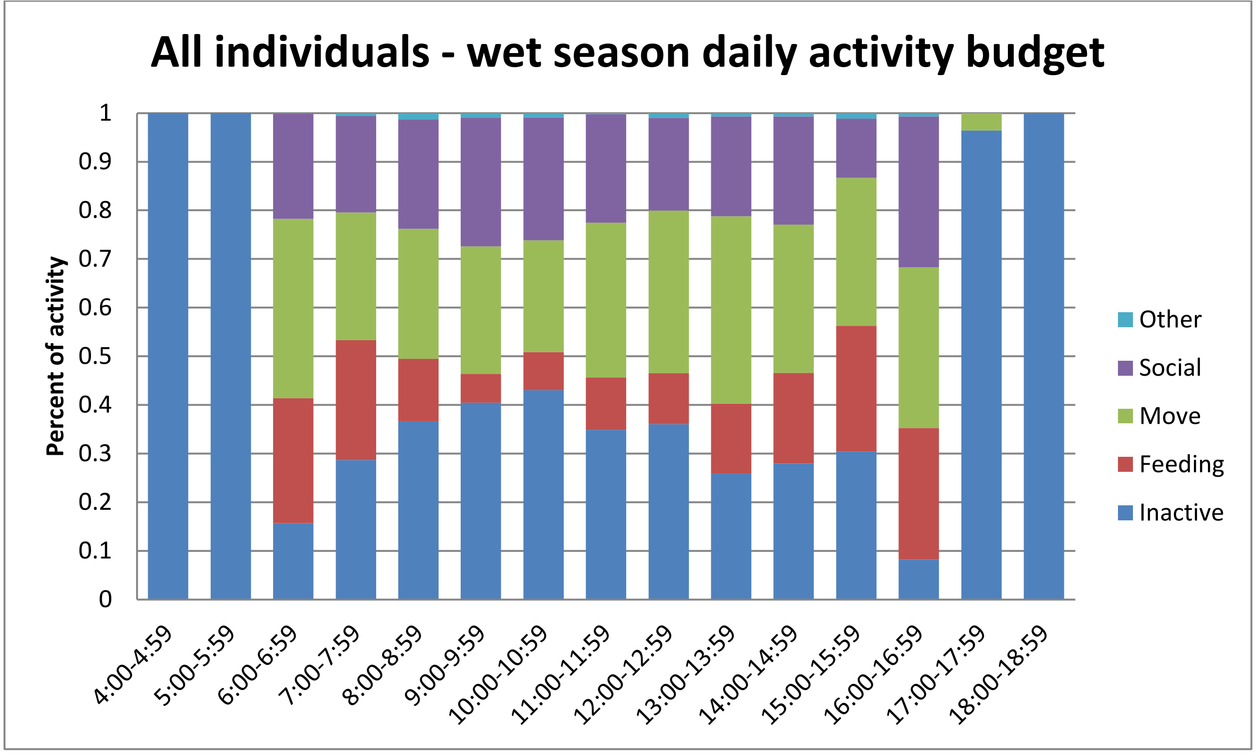


Figure 6.44. Wet season daily activity budget in all individuals.



6.3.5. Other behaviors

6.3.5.1. Copulation

There were six observed copulation events, and these were not evaluated in the activity budget analyses because the sample size is too small for statistical analyses. These observations are briefly reviewed here.

Of the six observations, two occurred in the dry season during March and April, and four occurred in the wet season, once in June, twice in October, and once in December). Three of the six events were observed in the primary research group, four occurred when units were fused, and copulation lasted between two and 20 seconds. I only observed the adult females prior to mating in three events, and all three times the adult female presented to the adult male. All mating events occurred between 7:34 and 9:55.

6.3.5.2. Observations of terrestrial behavior

There were two observations of individuals on the ground, both occurring in February, but once in 2010 and once in 2011. The first involved an adult male who appeared to be feeding. The second involved a sub-adult male feeding on leaves of a sapling. February is the driest month on Son Tra, with zero to only a few cm of rainfall. An increase in terrestrial behaviors might relate to water stress and the reported February increase in range use (Chapter 5).

6.4. Discussion

6.4.1. Comparing activity budgets

6.4.1.1. Annual results – all individuals

Inactivity in this study was 35.3% of the activity budget. This is similar to the frequency of inactivity in grey-shanked doucs (37.0%) in central Vietnam (Ha Thang Long, 2009), red-shanked doucs (32.7%) in Laos (Phiapalath (2009), and black-shanked doucs (43.0%) in southern Vietnam (Hoang Minh Duc, 2007). This is also similar to *Rhinopithecus avunculus* (23% to 32%), *R. roxellana* (36%), and *R. bieti* (33% to 35%), and *Colobus angolensis* (32% to 44%) (see Chapter 2). Inactivity is generally common among colobines (Chapter 2).

Feeding in this study was 13.7% of the activity budget, which is again comparable to feeding percentages of activity budgets for grey-shanked doucs (11.9%) (Ha Thang Long, 2009), *R. avunculus* (15% to 18%) and *Trachypithecus p. leucocephalus* (13% to 17%) (see Chapter 2). Feeding is generally a more common activity in colobines (Chapter 2), and reasons for the reduced frequency of feeding in this study are discussed below.

Moving in this study was 28.6% of the activity budget, and this again is similar to the moving budget for grey-shanked doucs (25.8%) (Ha Thang Long, 2009) and red-shanked doucs in Laos (23.2%) (Phiapalath &Suwanwaree, 2010). This is also similar to *C. angolensis* (20% to

24%), *Rhinopithecus avunculus* (20% to 40%), and *R. roxellana* (23%) (see Chapter 2). Moving in most colobines is generally a less common activity (Chapter 2), and reasons for the increased frequency of moving in this study are discussed below.

Social behaviors in this study were 21.7%, and this is similar to the grey-shanked doucs (25.1%) (Ha Thang Long, 2009), *R. avunculus* (9% to 24%), and *T. p. leucocephalus* (18%) (see Chapter 2). Social activity is generally a less common activity in colobines (Chapter 2), and reasons for the increased frequency of social activity in this study are discussed below.

Self-grooming in this study was 0.7% of the activity budget, which is comparable to most colobines (Chapter 2).

In summary, the activity budget in this study is consistently comparable to grey-shanked doucs. Both this study and the grey-shanked douc study were in central Vietnam, and therefore variables characteristic for this region probably influence this similarity.

6.4.1.2. Annual results – adult and young individuals, adult males and adult females

In this study, adults vocalized significantly more than young individuals, and young individuals played significantly more than adults. Young individuals typically play more than adults, and the high frequency of vocalizations among adults further supports the importance of vocalizations in unit cohesion and coordination (Chapter 5). These results differ from other *Pygathrix* studies. In the grey-shanked doucs, adults fed more than younger individuals, who rested and socialized more than adults (Ha Thang Long, 2009). In black-shanked doucs in Vietnam, adults fed less than younger individuals, but socialized more (Hoang Minh Duc, 2007). In black-shanked doucs in Cambodia, adults socialized more and were more inactive than young individuals, who fed and moved more than adults (Rawson, 2009). None of these differences were statistically significant in this study at the annual scale of analysis.

In this study, adult males were significantly more vigilant than adult females, and adult females allogroomed significantly more than adult males. The higher frequency of allogrooming among adult females suggests allogrooming is important among adult females in creating and maintaining bond formations within and between family units (Chapter 5). The higher frequency of vigilance among adult males indicates they remain alert, although they also decrease vigilance when units are fused. For the grey-shanked doucs, adult males were also significantly more vigilant, but they also fed, moved and rested less than adult females (Ha Thang Long, 2009). Among black-shanked doucs in Cambodia adult males socialized more than adult females (Rawson, 2009).

6.4.1.3. Seasonal, monthly, and daily results

In this study, adults vocalized significantly more than young individuals in both the wet and dry seasons, and young individuals played significantly more than adults. These results were also found along the annual scale of analysis. Increased play behavior among young individuals is typical among primates. The increase of vocalizations among adults supports the importance of vocalizations to intragroup bond formation and unit coordination, and intergroup resource defense.

In this study, young individuals were significantly more social in the wet season then in the dry season. This is likely related to the degree of unit cohesion. In the wet season there is more fissioning and fusing. Each times units fuse, the younger individuals (infants and juveniles) tend to play with each other. This correlation was not supported on the monthly scale of analysis because young individuals also play when units are fissioned.

In this study, adult males were significantly more vigilant than adult females in the wet season, as they were along the annual scale of analysis. During the dry season, adult males were significantly more social than adult females. Yet, there was no significant difference in any social activity subcategory, indicating that they do not simply increase displays or vocalizations (as shown in the monthly correlation analysis with leaf flush), but they increase social activity in general. This suggests that when units tend to be more often fused (dry season) adult males remain more active, and when units are more often fissioned adult males remain more vigilant.

Last, adult females allogroomed significantly more than adult males in the wet season. During the wet season there is a greater degree of unit fission and fusion. As with play behaviors in young individuals, each time units fused adult females tended groom each other, their infants and other infants, highlighting the importance of bond formation among adult females. This correlation was not supported on the monthly scale of analysis because females also groom when units are fissioned.

Results of this study are more refined, but differ from results in other *Pygathrix* studies. For instance, Hoang Minh Duc (2007) reported the black-shanked doucs in Vietnam fed significantly more in the dry season, and rested significantly more in the wet season. The same pattern was reported for the black-shanked doucs in Cambodia (Rawson, 2009), and grey-shanked doucs in central Vietnam (Ha Thang Long, 2009). Conversely, Phaipalath & Suwanwaree (2010) noted the red-shanked doucs in Laos tended to feed and rest more in the wet season, although significance was not tested. In this study, feeding and resting did not fluctuate seasonally.

No previous study on *Pygathrix* has analyzed activity budgets on a monthly scale in relation to external variables, and therefore no comparison with other studies is possible. Daily activity budgets reported in grey-shanked and black-shanked doucs (Ha Thang Long, 2009; Hoang Minh Duc, 2007; Rawson, 2009) are similar to the daily activity budget observed in this study.

6.4.2. Influencing factors

6.4.2.1. Group size, ranging, and activity budgets

Pollard & Blumstein (2008) illustrated that resting time and group size were positively correlated. In this study resting significantly increased when units were fused, therefore resting is also correlated to group size.

Saj & Sicotte (2007), Teichroeb et al. (2003) and Teichroeb & Sicotte (2009) illustrated scramble competition among *Colobus vellerosus* reporting intragroup feeding competition increases with group size, necessitating increases in travel and/or feeding time to meet daily nutritional requirements (*i.e.*, the ecological-constraints model).

In this study, variations in the use of home range and daily path lengths were not correlated to variations in unit cohesion (see Chapter 5), suggesting that if scramble competition influenced douc behavior it did not significantly affect ranging patterns. Feeding competition can also be analyzed by comparing feeding activity with unit cohesion. In the annual, seasonal and monthly analyses these correlations were not significant. Units associate daily and on a daily scale the pattern of fission-fusion is significantly correlated to feeding, vocalizing and vigilance which all increase when units are fissioned, and significantly correlated with resting which increased when units are fused (section 6.3.4.2). Daily patterns in feeding and fission-fusion appear to be an adaptation in avoiding scramble competition.

6.4.2.2. Habitat and activity budgets

In this study, the percentage of feeding as part of the activity budget was low compared to most other colobines. Zhaoyuan Li & Rogers (2004) suggested that the low percentage of feeding in *T. p. leucocephalus* was related to high quality foods that were generally available throughout the year. They compared activity budgets between groups in high quality and low quality habitats, and found that the group in high quality habitats spent less time feeding.

On Son Tra, high quality foods are available throughout the year (Chapter 4). This may be the reason for the relatively low percentage of the annual activity budget spent on feeding.

The five dominant tree families on Son Tra were Dipterocarpaceae, Euphorbiaceae, Myrtaceae, Sapindaceae and Anacardiaceae (Chapter 3). Black-shanked doucs in Cambodia inhabit an entirely different habitat type, consisting of a drier and deciduous forests dominated by Lythraceae, Fabaceae, and Tiliaceae (Rawson, 2009). The habitat of the black-shanked doucs in Nui Chua Nature Reserve is relatively flat, and has a more arid and deciduous forest with a lower density of trees than Son Tra (Hoang Minh Duc, 2007). Black-shanked doucs in Phuoc Binh National Park inhabit more humid and evergreen forests that are comparable to Son Tra, which are dominated by Sapindaceae and Myrtaceae families. Grey-shanked doucs in Kon Ka Kinh National Park inhabit forests similar to Son Tra with comparable tree height, density, and composition (Ha Thang Long, 2009). The forest is humid and evergreen, and the five most common tree families are Myrtaceae, Sapindaceae, Euphorbiaceae, Lauraceae and Guttiferae.

The overall percentages in the annual activity budget in this study were comparable to the activity budget of grey-shanked doucs, just as the forests of Son Tra and Kon Ka Kinh are also most comparable. Habitat similarities may therefore influence activity budget similarities as has previously been illustrated by Isbell (1991) who noted that the distribution and abundance of food resources influence daily movements and activity patterns. However, different activity budgets have been reported within single populations or in animals living in the same environment (see Chapter 2; see also Firoj-Jaman & Huffman; 2008; Isbell & Young, 1993), and it can be assumed that habitat variables are not the only influencing factor.

6.4.2.3. Climate and activity budgets

Several studies have shown that temperature and seasonality influence primate activity budgets (Dunbar, 1992; Hanya, 2004; Kosheleff & Anderson, 2009; Williamson & Dunbar, 1999). Dunbar (1988) suggested primates in tropical environments need to rest during daily temperature peaks to reduce thermoregulatory stress. This pattern has been found in all *Pygathrix* studies. Dunbar (1992) reported *Theropithecus gelada* in more seasonal environments increase feeding times compared to those in less seasonal environments to compensate for the thermoregulatory costs. Hayna (2004) observed *Macaca fuscata* decrease traveling and feeding in cooler temperatures as a means to conserve energy. Kosheleff & Anderson (2009) illustrated that *Pan troglodytes schweinfurthii* increase terrestrial and resting behaviors in warmer temperature as an adaptation to thermoregulation. If temperatures fall below the thermoneutral values, energy-consuming activity is reduced as a means to conserve energy. If temperatures increase above thermoneutral values, temperature-generating activity is reduced likewise to conserve energy, which otherwise has to be spent on cooling the body. Therefore, differences and similarities in climate variables between *Pygathrix* studies may also explain activity budget variations.

The climate on Son Tra is mild with minimal fluctuation in temperature throughout the year (Chapter 3). Monthly average temperatures on Son Tra never drop below 21.5°C and never increase above 29.5°C. In Kon Ka Kinh National Park (grey-shanked doucs), monthly average temperatures ranged from 20°C to 27.5°C (Ha Thang Long, 2009), similar to Son Tra. In contrast, temperatures in the habitat of black-shanked doucs in Cambodia ranged between 18.8° to 32.8°C (Rawson, 2009). In Phuoc Binh temperatures were noted as often reaching below 15°C during six months of the year (Hoang Minh Duc, 2007). Higher percentages of inactivity in these black-shanked douc studies could be an adaptation to thermoregulation. Red-shanked doucs in Son Tra and grey-shanked doucs in Kon Ka Kinh probably experience less thermoregulatory stress and therefore are less concerned about conserving energy, permitting for increased activity.

Although the temperatures on Son Tra are not extreme enough that activity budgets on the annual scale are influenced by energy saving considerations, temperatures still influence behavior on the daily and monthly scale. In this study, adult males and adult females significantly increased vigilance and self-grooming with increases in temperature, and significantly increased resting and decreased self-grooming with decreases in temperature. Young individuals vocalized significantly less when temperatures were cooler, and played and allogroomed significantly more when temperatures were warmer. Temperature therefore significantly influences activity budgets in the doucs, which adapt to thermoregulatory stresses by increasing resting, and for young individuals by decreasing energetically expensive behaviors (*i.e.* play).

6.4.2.4. Vigilance and vocalizations: influences of predation, resource defense, and unit coordination (modularity)

Predation risk influences behaviors and activity budgets, especially the degree of vigilance and alarm calling (Cords, 1990; Cowlishaw, 1997; Enstam, 2007; Hill & Weingrill, 2007; Isbell, 1994; Treves, 1999).

Vigilance has been shown to decrease with group size in many mammals and birds due to the reduced individual risks in not detecting a predator, called the “many eyes” hypothesis (Burger & Gochfeld, 1992; Elgar, 1989; Isbell & Young, 1993; Lima, 1995; Quenette, 1990; Roberts, 1995). In contrast, Treves (1999) suggested vigilance can increase with group size due to surveillance of conspecifics. In this study, vigilance significantly increased when units were fissioned and significantly decreased when they were fused, which conforms to the “many eyes” hypothesis. Additionally, habitat type affects the type of predator avoidance behavior and the degree of vigilance, and vigilance increases in more dense and closed habitats (Enstam, 2007; Isbell, 1994; Sharpe & Van Horne, 1998).

Zuberbuhler et al. (1999) illustrated alarm calls are an important predator deterrent by alerting an ambushing predator that it has been detected, and there are several such predators to infant and small juvenile doucs on Son Tra (Chapter 5 and appendices). Hamilton (1971) reported that vocalizations also recruit conspecifics to a threat, and this is an additional predator deterrent. As discussed in Chapter 5, alarm calling in doucs consistently evoked other intragroup units to respond with alarm calls, and when units were fissioned calls were accompanied by cooperative behaviors including the responding unit moving towards the calling unit (recruiting), or the calling unit fleeing from a threat towards the responding unit. Vocalizations in doucs therefore appear to be used to initiate cooperative defense responses and serve in unit coordination as is seen in other primates (Wheeler, 2008).

Calls might also play a role in mate defense and sexual selection given that male loud calls in some primates announce mate quality (see Chapter 5). In this study, adults vocalized significantly more than young individuals which may partly relate to quality advertisement and mate defense.

The increased social activity, especially vocalizations, in the red-shanked doucs in this study is possibly influenced by predation risk, intragroup unit coordination, intergroup resource defense, and the density of Son Tra forests.

6.4.2.5. Moving, diets, and ranging

Oates (1987) suggested that diets rich in widely available resources (e.g. leaves) require less traveling. If this is applicable to *Pygathrix*, it is distinctive that the red-shanked doucs in this study and the grey-shanked doucs of Kon Ka Kinh showed higher moving budgets compared to the black-shanked douc studies in more seasonal, deciduous habitats. In the grey-shanked doucs the high moving budget might be related to their significantly larger home ranges compared to other *Pygathrix* studies. This could sufficiently explain the increased moving budget in Kon Ka Kinh. However, home range size in *Nasalis larvatus* is as large as in grey-shanked doucs, but is accompanied by a reduced (4%) moving budget (Chapter 2).

The increased moving and social budgets in this study and in Kon Ka Kinh accompany a decreased percentage of feeding as part of the activity budget compared to other colobines. This implies that energy intake even with a reduced feeding percentage is still adequate to meet increased energy demands, suggesting an annual availability of high quality foods.

C. angolensis had a comparable moving budget, but they traveled over significantly greater distances and have significantly larger home ranges than the red-shanked doucs on Son Tra. The habitat of *C. angolensis* is characterized by high quality mature foliage (Fimbel et al., 2001), but these resources may have long renewal times necessitating increases in travel. A similar explanation likely does not account for the high moving budget in the red-shanked doucs on Son Tra. The climate on Son Tra remains fairly mild and humid throughout the year, which would support consistent plant development, higher quality mature foliage, and fast regeneration rates due to optimal growing conditions. A more likely explanation is the influence of intragroup scramble competition and the need to move more in order to avoid competition between units, and avoid exhausting keystone resources.

6.5. Conclusion

In summary, the activity budget among red-shanked doucs consists of inactivity (35.3%), moving (28.6%), sociality (21.7%), feeding (13.7%) and other (0.7%). Several differences were observed between seasons and groups of individuals. Only significant results are summarized here.

On the annual scale, adults vocalized more than young individuals, and vocalized frequently in general, highlighting the importance of vocalizations within the modular society of doucs on Son Tra. Young individuals played more than adults. Adult males were significantly more vigilant than adult females, and females allogroomed significantly more than males, both highlighting the importance of intragroup bond formations and communication.

On the seasonal scale, adults vocalized more than young individuals in both seasons, and young individuals played more than adults in both seasons. Young individuals were more social in the wet season, and adult females allogroomed more than males in the wet season, both possibly related to the increased degree of fission-fusion behavior in the wet season, and the strengthening or maintenance of bond formations between family units each time fusion occurs. Adult males were more vigilant than adult females in the wet season, and this also partly relates to the increased degree of fission-fusion in the wet season, as vigilance significantly increases when units are fissioned. Lastly, adult males were more social in the dry season than adult females, relating to the increase in vocalizations and displaying during peaks in leaf flush.

On a monthly scale, moving was positively correlated to temperature and negatively correlated to flowering in all individuals. In all individuals, traveling positively correlated to variation in the use of home range, displaying was positively correlated to leaf flush, and vocalizations were negatively correlated to leaf flush. Adults followed these patterns with the addition of self-grooming being positively correlated to temperature. In young individuals, vocalizations were negatively correlated with temperature, playing was positively correlated with temperature, and allogrooming was positively correlated with flowering. In adult males self-grooming was positively correlated to temperature, moving was negatively correlated to flowering, traveling was positively correlated to variations in the use of home range, displays were positively correlated to leaf flush, and vocalizations were negatively correlated to leaf flush. In adult females self-grooming was positively correlated to precipitation, moving was positively correlated to temperature and variation in the use of home range, and moving was negatively correlated to flowering.

Daily, the doucs followed a typical *Pygathrix* pattern, and exhibited a daily fission-fusion pattern which was significantly correlated to the daily activity budgets. When units were fused they rested significantly more and when units were fissioned they moved, fed, and vocalized significantly more, and were significantly more vigilant. This appears to be an adaptation to avoiding scramble competition, and to maintaining contact and coordination between dispersed foraging units.

Finally, the activity budget of red-shanked doucs in this study was most comparable to grey-shanked doucs in Kon Ka Kinh, including the high percentage of social activity, the low percentage of inactivity especially resting, and the low percentage of feeding. Reasons for this similarity might be related to habitat and climatic characteristics in central Vietnam. Increased vigilance and vocalizations might also be related to these characteristics, and to predation risk, resource defense, and unit coordination. Lastly, habitat characteristics and scramble competition appear to influence the moving budget.

Chapter 7. Feeding ecology: food choice, selectivity, and quality

7.1. Introduction

7.1.1. Chapter preview

This chapter analyzes the variation in the selection of plant species, categories, and parts between seasons, months, and individuals, and in relation to weather and phenology.

The introduction provides a review of feeding ecology in *Pygathrix* followed by the methods of data analysis. Results are divided into six sections. The first section presents annual analyses, the second presents seasonal analyses, and the third presents monthly analyses. These first three sections are each composed of three subsections, including analyses of food categories, leaf ages, and leaf parts. The forth section reports on nursing, the fifth section reports food species, and the last section reports chemical and nutritional data. Finally, the discussion compares the results to previous *Pygathrix* studies and other feeding ecology approaches.

7.1.2. Review of feeding ecology in *Pygathrix*

Leaves are among the most commonly selected food item reported in *Pygathrix* studies, although fruits and seeds may dominate the diet seasonally. Of the consumed leaves, young leaves are most commonly selected.

Lippold (1998) reported red-shanked and black-shanked doucs fed mostly on leaves (82%), followed by fruits and seeds (14%), and flowers (4%). Of the consumed leaves most were young (75%). Pham Nhat (1993a) estimated that doucs consumed 63% leaves and 37% fruits and seeds. Otto (2005) noted captive doucs selected young leaves most often during feeding.

Hoang Minh Duc (2007) reported the black-shanked doucs in southern Vietnam fed mostly on leaves (54%), followed by fruit and seeds (29%), flowers (15%) and other items (1%). He found that young leaves were preferred over mature leaves. In the dry season, leaf and flower consumption increased (60% and 20%), and fruit and seed consumption decreased (17%). In the wet season, leaves remained a common dietary item (52%), fruit and seed consumption increased (34%), and flowers consumption decreased (13%).

Rawson (2009) observed that black-shanked doucs in Cambodia fed most frequently on fruit and seeds (51%), followed by leaves (40%), flowers (9%) and other items (0.1%). He noted that of the consumed leaves, young leaves were most commonly selected (60%). In the dry season, leaf and flower consumption increased (42% and 15%), but seeds and fruits remained the more commonly consumed items (44%). In the wet season, fruit and seed consumption increased (58%), and leaf and flower consumption decreased (38% and 4%). Massive logging was also noted in the area, which may have affected the ratio of food trees exploited for their leaves to food trees exploited for their fruit and seeds.

Ha Thang Long (2009) reported the grey-shanked doucs in Kon Ka Kinh National Park fed mostly on leaves (59%) followed by fruit and seeds (41%), with flowers and other items rarely eaten. Of selected leaves, most were young (84.7%). In the dry season, consumption of leaves increased (88%), and fruit and seed consumption decreased (12%). In the wet season, fruit and seed consumption increased (69%), and leaf consumption decreased (31%).

Phiapalath et al. (2011) did not report annual percentages for the red-shanked doucs in Laos, but reported on seasonal differences. During the dry season, consumption of leaves increased (80%), and fruit and seed consumption decreased (9%). In the wet season, fruit and seed consumption increased (54-57%), and leaf consumption decreased (21-39%).

Rawson (2009) illustrated that selection of young leaves, fruits, seeds, and flowers was not correlated to food availability in black-shanked doucs. Ha Thang Long (2009) observed however that the selection of young leaves was significantly and positively correlated to availability. Both Ha Thang Long (2009) and Phiapalath (2009) noted tendencies for increased fruit selection with increased availability, but these correlations were not significant.

Otto (2005) first reported on chemical and nutritional influences in food selection in doucs, noting that young leaves were preferred, which were enriched in protein and lower in fiber than mature leaves. In the one case where mature leaves were preferred, it had higher protein and lower fiber content than other mature leaves. The least selected plants had the highest fiber and lowest protein content. She also found that the tannin content did not differ between selected and non-selected leaves. O'Brien (2006) reported grey-shanked doucs in captivity selected foods significantly higher in protein than non-selected foods, and confirmed that tannin content did not differ between selected and non-selected food items. In contrary, Hoang Minh Duc (2007; et al., 2011) reported selected and non-selected foods of black-shanked doucs in southern Vietnam did not significantly differ in protein, fiber, tannin, or most micronutrient contents. Nguyen Thi Tinh et al. (2012) similarly reported selected and non-selected leaves of grey-shanked doucs in central Vietnam did not significantly differ in fiber or protein content.

7.2. Methods of data analysis

In this study there were 4,155 feeding records of which over 40% were unidentified food items (Table 7.1). These "unidentified" items were likely leaves except in May they were most likely flowers. Additionally, nursing is only relevant to infants. These two food categories (unidentified foods and nursing) are removed from the analyses, resulting in 2,426 feeding records.

Feeding is divided into four categories (Chapter 3), including fruits and seeds, flowers, leaves, and bark/pith. Leaves were divided into two subcategories including age (mature and young) and part (whole blade, apex, base, or petiole). The monthly percentage of selection for each variable is compared to phenology and weather variables with Pearson's Correlation coefficient, two-tails with p=0.05. These correlations relate feeding data to transect data, not to food tree data specifically. Most transect trees were not identified beyond family level, and it is not possible to relate behavior to feeding tree phenology more specifically. However, given the importance of *Parashorea stellata* in the diet of the doucs, and that nearly all transect dipterocarp trees were *P. stellata*, it is possible to relate feeding patterns specifically to the leafing and flowering phenology of *P. stellata* (Chapter 4). The monthly percentage of selection of young leaves and flowers is compared to *P. stellata* phenology with Pearson's Correlation coefficient, two-tails with p=0.05.

Analyses are conducted for all individuals (N=2,426), comparisons between adult males and adult females (N=1,011 and 1,086), where sample size permits comparisons between young individuals and adults (N=250 and 2,097), and comparisons between seasons are all conducted with chi-square, two-tails, using Yate's correction and the contingency coefficient, at p=0.05. As noted in Chapter 6, Yate's correction is used due to the large sample size. Also, the contingency coefficient (C) was used on all significant chi-square tests as a means to enhance the statistical tests. Due to the large sample sizes there is an increased likelihood of producing statistically significant results without the existence of a meaningful relationship between the tested variables, and C provides a statistical correction. The C-value, as a percentage of C-max, allows for an additional measure of the degree of association between variables. In this study, only significant chi-square tests that also have a C-value of 25% (0.25) or greater are considered significant and reported. All other significant chi-square tests are not considered significant and are not reported in the text, although they are reported in Table 7.7 at the end of section 7.3.2 of this chapter.

Non-significant results are generally not reported. There is an adult sampling bias, but no bias between adult females and adult males.

Sixty-two food species were identified, of which 44 were identified from observations of douc groups on Son Tra during the main research activities, four were identified among the primary research group between June 2011 and November 2011 after the main research activities concluded, and 14 were selected by a confiscated adult male red-shanked douc who was trapped on Son Tra by poachers and kept in a cage at Son Tra ranger headquarters for three months. About 50 different species of plants were collected in Son Tra forests for this confiscated individual, out of which he selected twenty. Of those, six were later observed to be eaten among other groups living in the wild on Son Tra.

Chemical and nutritional analyses were conducted on 22 samples. Tests involved water, ash, condensed tannins, crude protein, neutral detergent fiber (NDF) and acid detergent fiber (ADF) (Chapter 3). Data is presented descriptively due to the small sample size, but a few statistical comparisons are conducted using unpaired two-tailed students *t*-test at p=0.05.

7.3. Results

7.3.1. Annual results

7.3.1.1. Food categories

Figure 7.1 and Table 7.1 show food category selection in all individuals. Leaves were the most common food item (87.8%), followed by fruits and seeds (10.2%), flowers (1.6%) and bark/pith (0.4%).

Figure 7.2 and Table 7.1 show food category selection in adult males, adult females, and unidentified individuals. Only adult males were observed to feed on bark/pith. Annual food category selection between adult males and adult females did not significantly differ. See Table

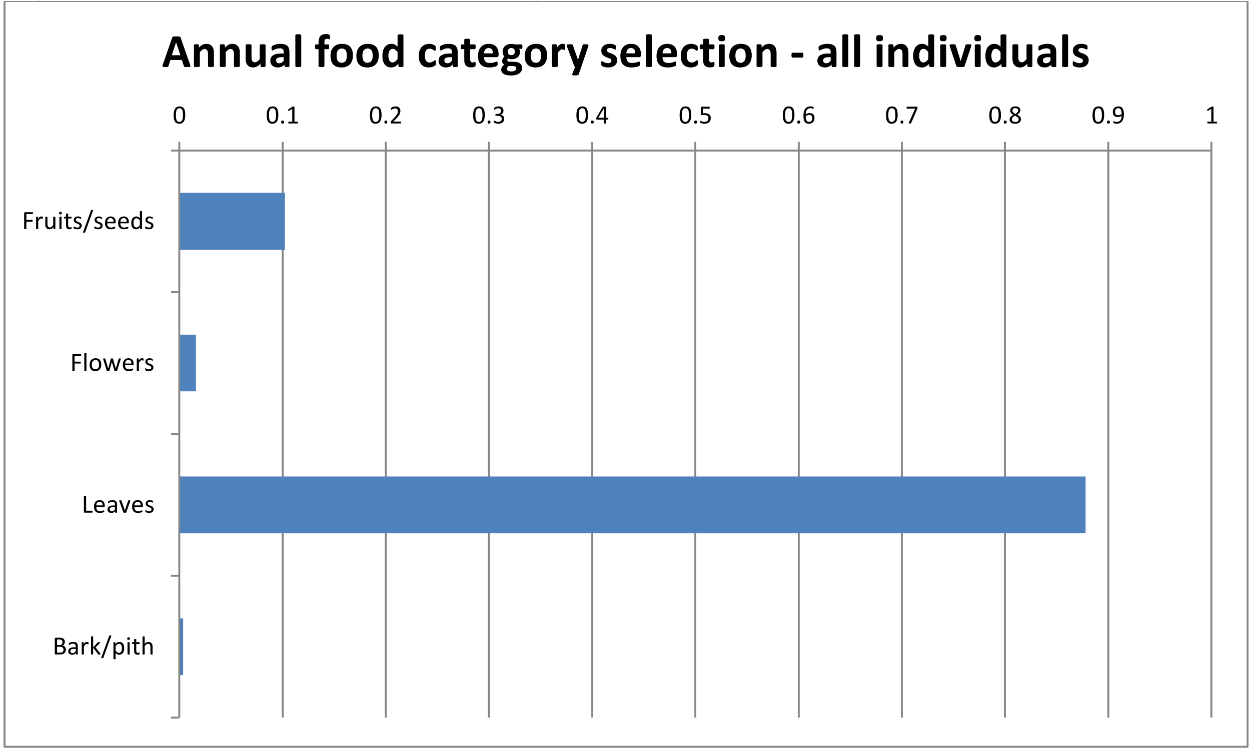
7.7 at the end of section 7.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Unidentified individuals more commonly fed on fruits and seeds than did adults. Young individuals (Table 7.1) are not analyzed or compared to adults because they were only observed to feed from leaves, aside from nursing.

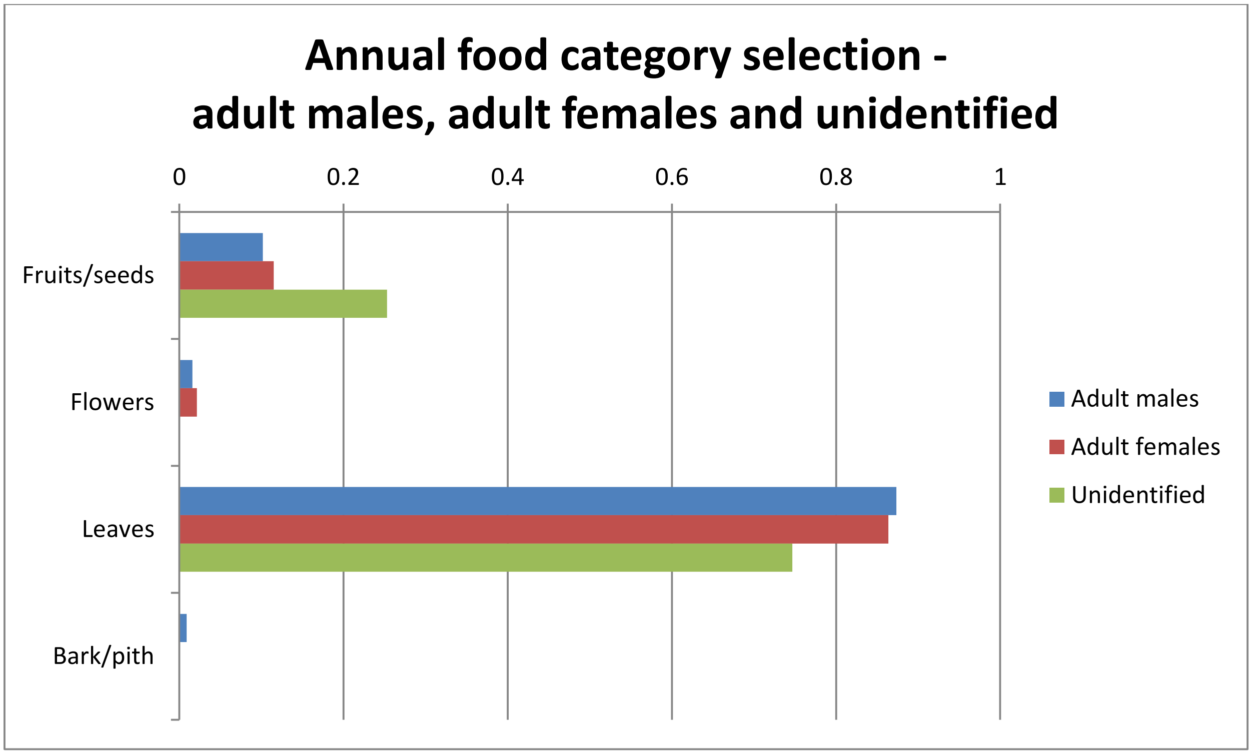
Table 7.1. Annual selection of food categories.
Fr/s=fruits and seeds, Fl=flowers, L=leaves, B/p=bark/pith, indet.=unidentified food items, and Br=breast feeding.

	All individuals			All individuals		Unidentified individuals		Young individuals		Adult males		Adult females	
	N	%		N	%	N	%	N	%	N	%	N	%
Fr/s	248	6.0	Fr/s	248	10.2	20	25.3	0	0	103	10.2	125	11.5
Fl	39	0.9	Fl	39	1.6	0	0	0	0	16	1.6	23	2.1
L	2130	51.3	L	2130	87.8	59	74.7	250	100	883	87.3	938	86.4
B/p	9	0.2	B/p	9	0.4	0	0	0	0	9	0.9	0	0
Indet.	1718	41.3	Total	2426		79		250		1011		1086	
Br	11	0.3											
Total	4155												

Figure 7.1. Annual selection of food categories in all individuals.



7.2. Annual selection of food categories in adult males, adult females, and unidentified individuals.



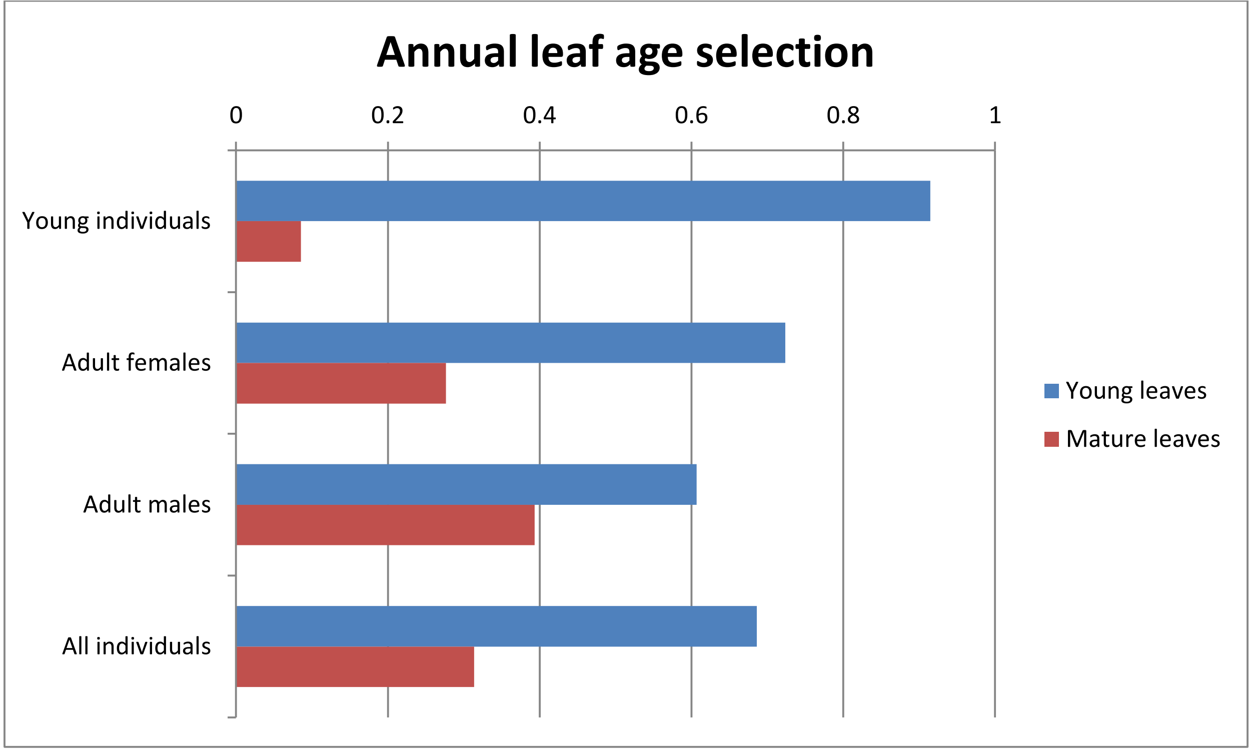
7.3.1.2. Leaf age

There are two subcategories for leaf age (*i.e.*, young and mature), and therefore their percentages are inverses and the chi-square results for young leaves are identical to results for mature leaves. In all individuals, 68.6% of selected leaves were young (Figure 7.3 and Table 7.2). There were no significant differences in the frequency of young leaf selection between adults and young individuals, or adult males and adult females. See Table 7.7 at the end of section 7.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Table 7.2. Annual leaf age selection.

	All individuals		Adults		Young		Adult males		Adult females	
	N	%	N	%	N	%	N	%	N	%
Young	844	68.6	724	66.7	107	91.5	321	60.7	403	72.4
Mature	386	31.4	362	33.3	10	8.5	208	39.3	154	27.6

Figure 7.3. Annual leaf age selection.



7.3.1.3. Leaf parts

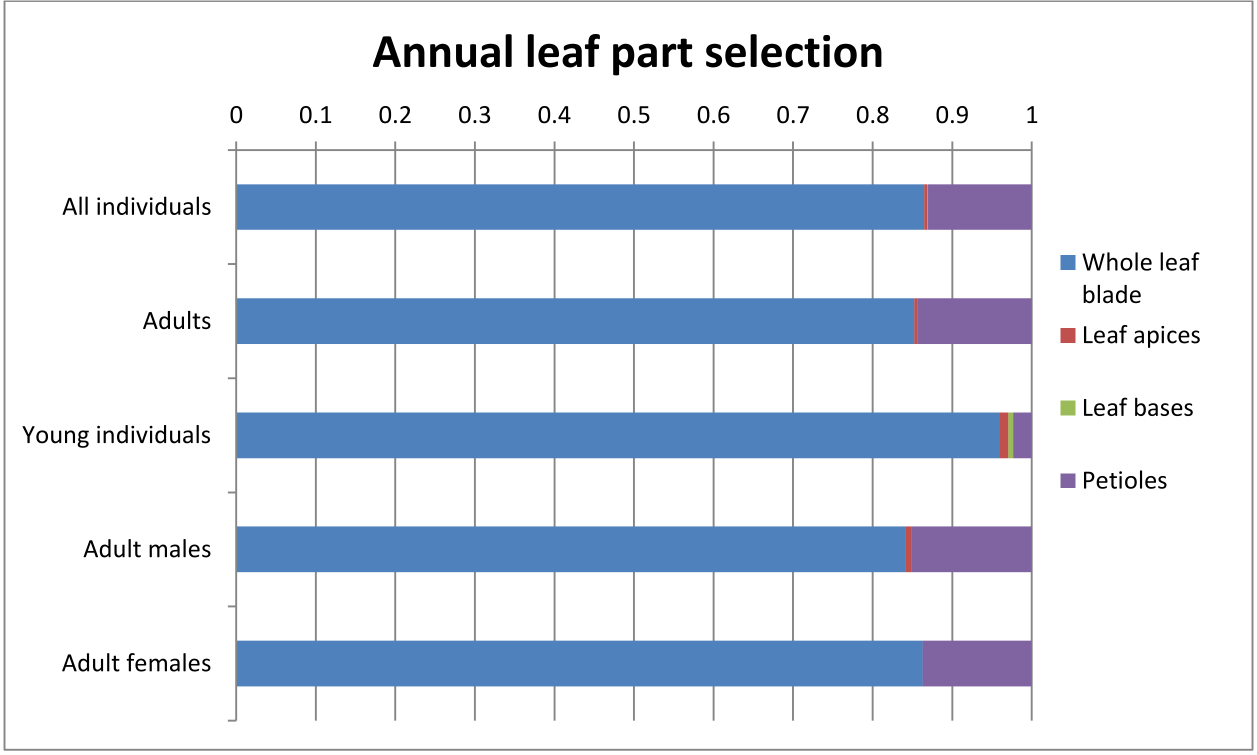
Leaf parts included four subcategories: whole leaf blades, leaf apices (upper part of the leaf blade), leaf bases (lower part of the leaf blade), and petioles. In all individuals, 86.5% of selected leaves were whole leaf blades, and 13.1% were petioles (Figure 7.4 and Table 7.3).

There were no significant differences in the selection of whole leaf blades or petioles between adults and young individuals, or adult males and adult females. Selection for leaf apices or bases was infrequent in adult males and young individuals, and absent in adult females, and was therefore not compared. See Table 7.7 at the end of section 7.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Table 7.3. Annual leaf part selection.

	All individuals		Adults		Young		Adult males		Adult females	
	N	%	N	%	N	%	N	%	N	%
Whole	1490	86.5	1289	85.3	164	95.9	628	84.2	661	86.3
Apices	7	0.4	5	0.3	2	1.2	5	0.7	0	0
Bases	1	0.1	0	0	1	0.6	0	0	0	0
Petioles	225	13.0	218	14.4	4	2.3	113	15.1	105	13.7

Figure 7.4. Annual leaf part selection.



7.3.2. Seasonal results

7.3.2.1. Food categories

Wet and dry season food category selection in all individuals is presented in Figure 7.5 and Table 7.4. There was no seasonality in the selection of leaves, fruit and seeds, flowers or bark/pith.

Figures 7.6, 7.7, and 7.8 illustrate seasonal patterns in adult males, adult females, and unidentified individuals. There was no seasonality in the selection of leaves, fruit and seeds, flowers or bark/pith in adult males or adult females. Additionally, there were no significant differences in leaf, fruit and seed, flower, and bark/pith selection between adult males and adult females in either the wet or dry season. See Table 7.7 at the end of section 7.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Table 7.4. Seasonal selection of food categories.

DRY SEASON								
	All individuals		Unidentified individuals		Adult males		Adult females	
	N	%	N	%	N	%	N	%
Fruit / seeds	109	10.2	9	20.9	47	11.4	53	12.0
Flowers	36	3.4	0	0	16	3.9	20	4.5
Leaves	917	85.7	34	79.1	342	82.8	370	83.5
Bark / pith	8	0.7	0	0	8	1.9	0	0
WET SEASON								
	All individuals		Unidentified individuals		Adult males		Adult females	
	N	%	N	%	N	%	N	%
Fruit / seeds	139	10.3	11	30.6	56	9.3	72	11.2
Flowers	3	0.2	0	0	0	0	3	0.5
Leaves	1213	89.4	25	69.4	541	90.5	568	88.3
Bark / pith	1	0.1	0	0	1	0.2	0	0

Figure 7.5. Seasonal selection of food categories in all individuals

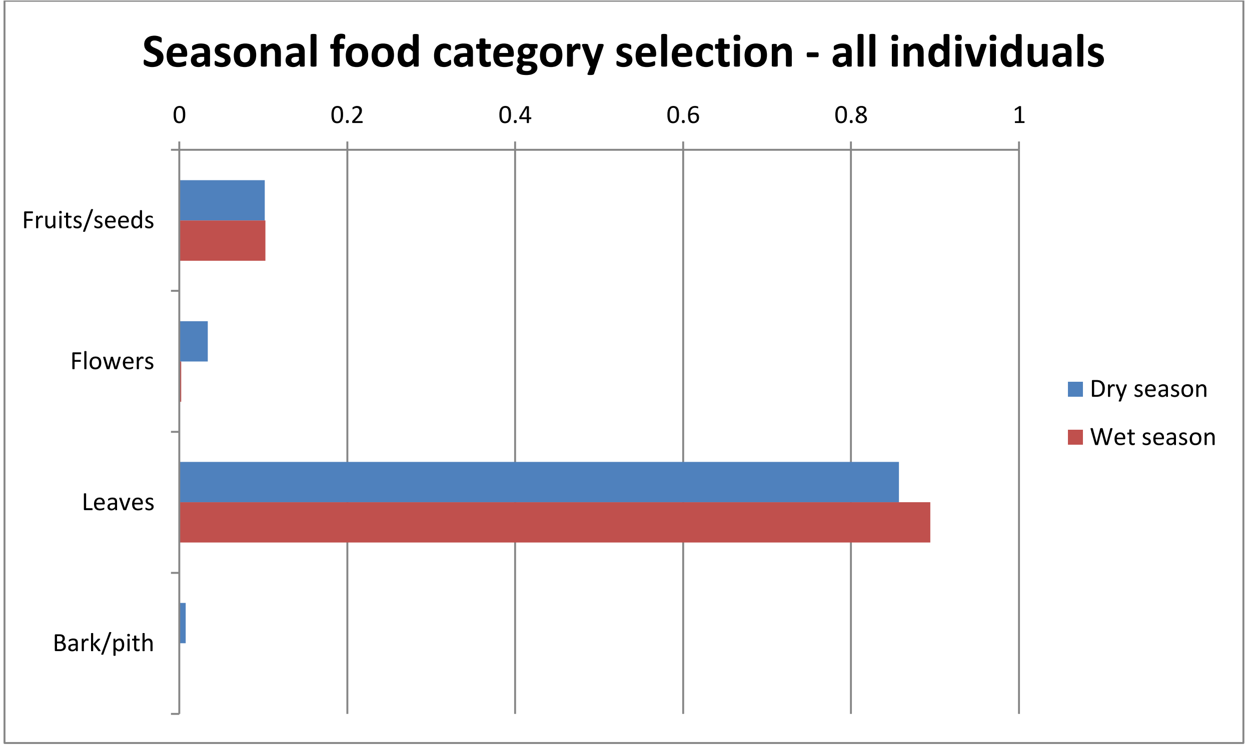


Figure 7.6. Seasonal selection of food categories in adult males.

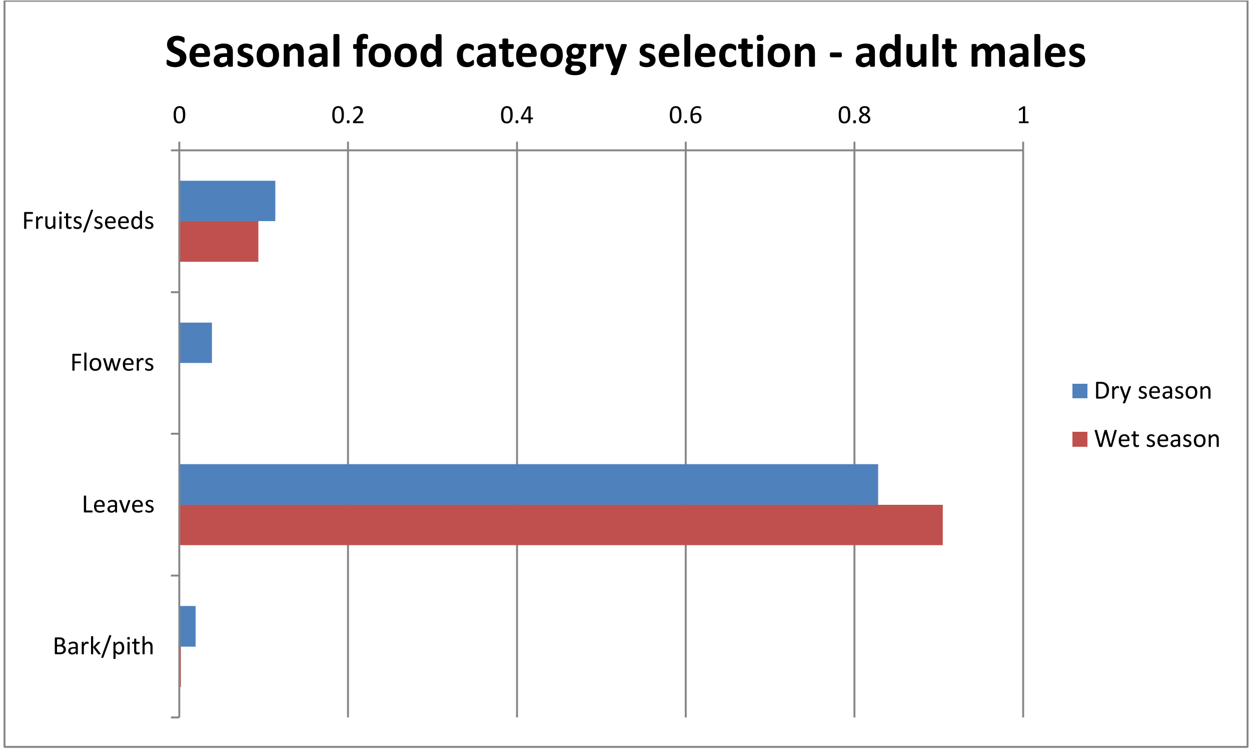


Figure 7.7. Seasonal selection of food categories in adult females.

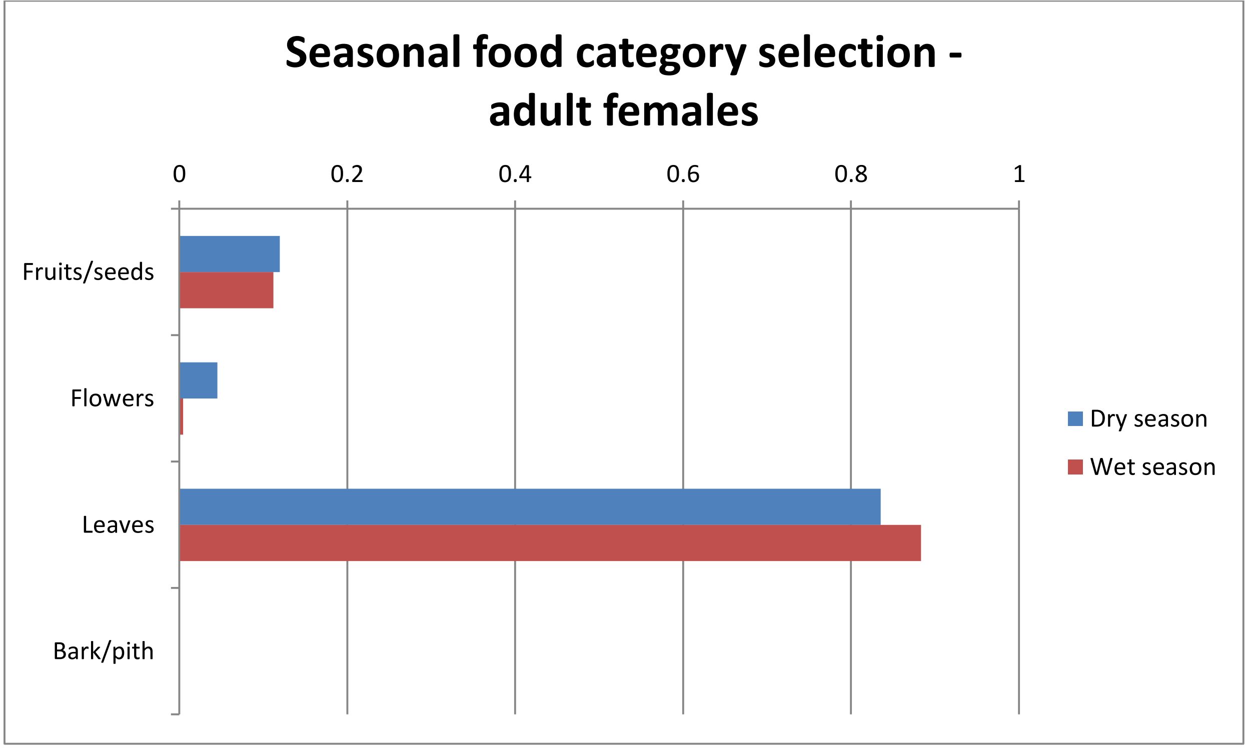
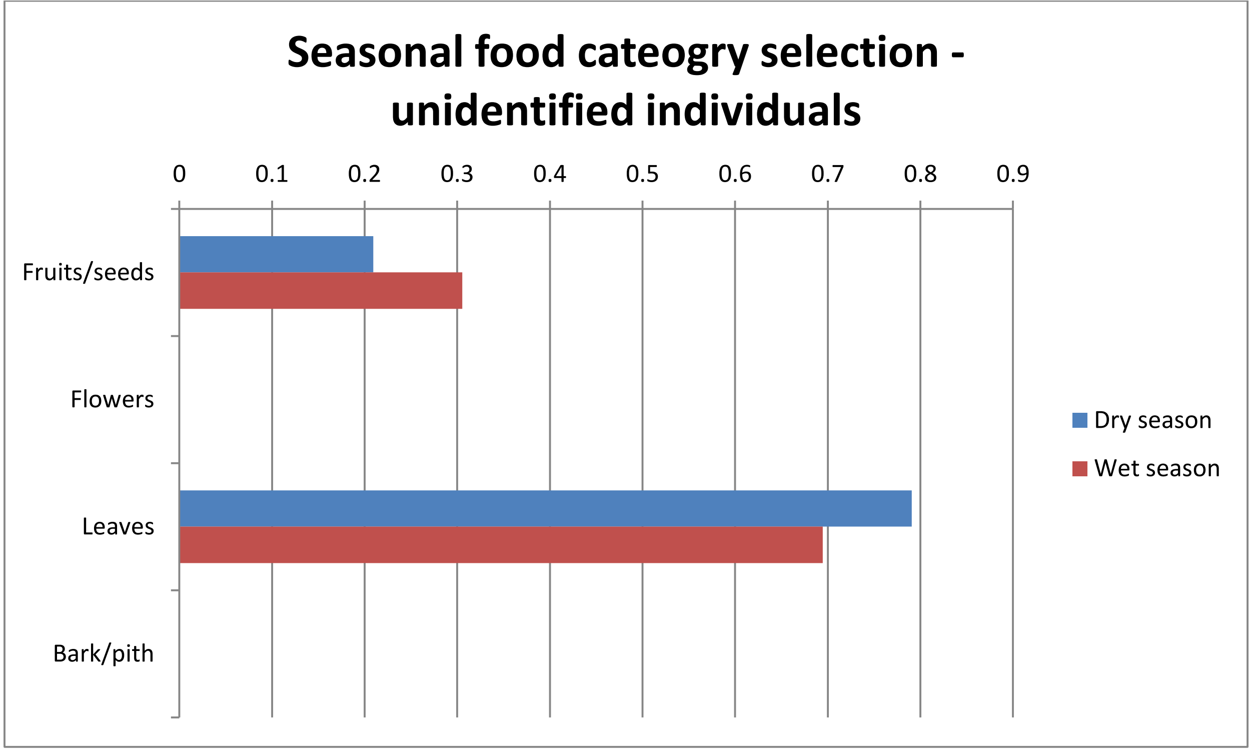


Figure 7.8. Seasonal selection of food categories in unidentified individuals.



7.3.2.2. Leaf age

There are two subcategories for leaf age (*i.e.*, mature and young), and therefore their percentages are inverses and the chi-square results for young leaves are identical to results for mature leaves. Figure 7.9 and Table 7.5 present this data in all groupings of individuals.

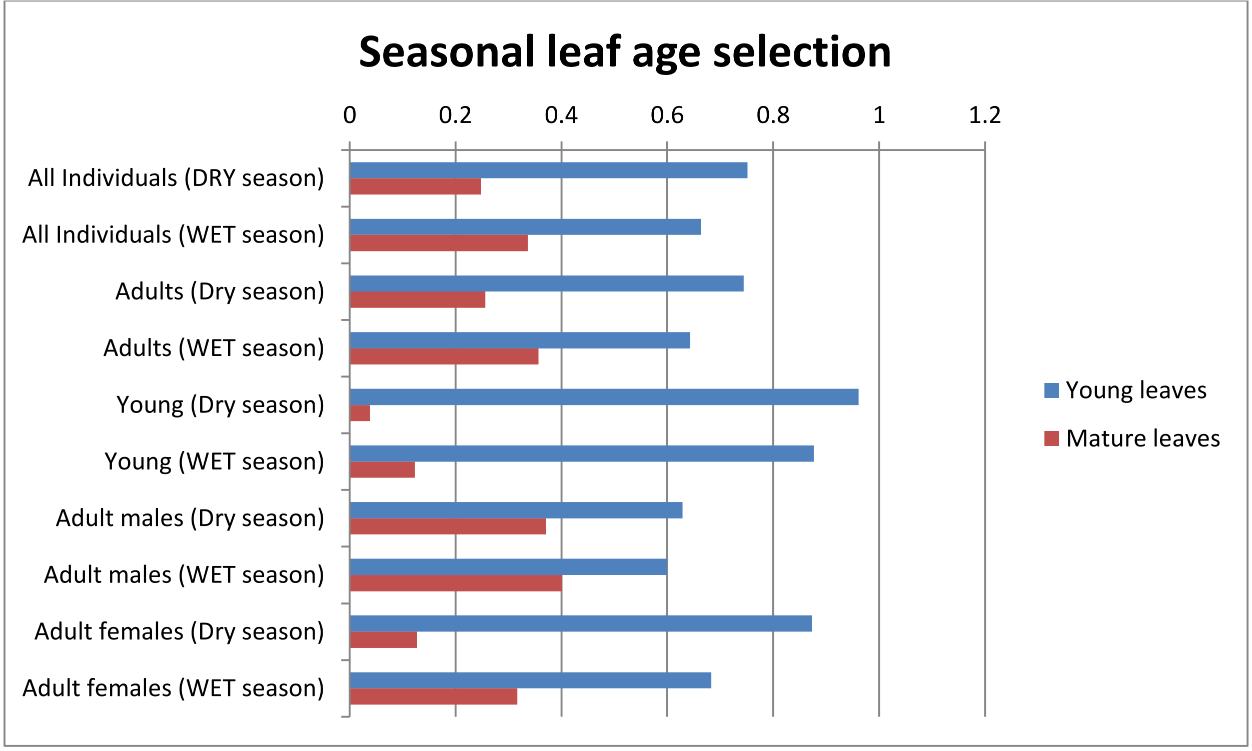
In all individuals, 75.2% of selected leaves in the dry season were young leaves, and in the wet season 66.3% were young. There were no significant differences in the selection of young leaves between seasons in all groupings of individuals.

Adult females selected young leaves significantly more than adult males in the dry season [$X^2(1, N=250) = 18.23$, $p<0.0001$, C=0.37]. There were no other significant seasonal differences between adults and young individuals, or adult males and adult females. See Table 7.7 at the end of section 7.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Table 7.5. Seasonal leaf age selection.

DRY SEASON										
	All individuals		Adults		Young		Adult males		Adult females	
	N	%	N	%	N	%	N	%	N	%
Young	239	75.2	186	74.4	50	96.1	83	62.9	103	87.3
Mature	79	24.8	64	25.6	2	3.9	49	37.1	15	12.7
WET SEASON										
	All individuals		Adults		Young		Adult males		Adult females	
	N	%	N	%	N	%	N	%	N	%
Young	605	66.3	538	64.4	57	87.7	238	59.9	300	68.3
Mature	307	33.7	298	35.6	8	12.3	159	40.1	139	31.7

Figure 7.9. Seasonal leaf age selection.



7.3.2.3. Leaf parts

Leaf parts are divided into their subcategories and selection of these parts is illustrated in Figure 7.10 and Table 7.6 in all groupings of individuals.

Whole leaf blades were selected significantly more in the dry season than in the wet season in all groupings of individuals except young individuals: all individuals [$X^2(1, N=1723) = 114.45$, p<0.0001, C=0.35], adults [$X^2(1, N=1512) = 107.89$, p<0.0001, C=0.37], adult males

[$X^2(1, N=746) = 34.57$, $p<0.0001$, C=0.30], and adult females [$X^2(1, N=766) = 78.3$, $p<0.0001$, C=0.43]. Similarly, petioles were selected significantly more in the wet season than in the dry season in all groupings of individuals except young individuals: all individuals [$X^2(1, N=1723) = 116.22$, $p<0.0001$, C=0.36], adults [$X^2(1, N=1512) = 109.58$, $p<0.0001$, C=0.37], adult males [$X^2(1, N=746) = 35.36$, $p<0.0001$, C=0.30], and adult females [$X^2(1, N=766) = 78.3$, $p<0.0001$, C=0.43].

There was no seasonal difference in leaf apex or base selection. There were no significant differences in the selection of whole leaf blades, apices, or petioles between adults and young individuals, or adult males and adult females, in both the wet and dry seasons. See Table 7.7 at the end of section 7.3.2 for additional comparisons that did not reach significance through the contingency coefficient.

Table 7.6. Seasonal leaf part selection.

DRY SEASON										
	All individuals		Adults		Young		Adult males		Adult females	
	N	%	N	%	N	%	N	%	N	%
Whole	734	96.4	616	96.4	105	99.1	304	93.3	312	99.7
Apices	2	0.3	2	0.3	0	0	2	0.6	0	0
Bases	1	0.1	0	0	1	0.9	0	0	0	0
Petioles	24	3.2	21	3.3	0	0	20	6.1	1	0.3
WET SEASON										
	All individuals		Adults		Young		Adult males		Adult females	
	N	%	N	%	N	%	N	%	N	%
Whole	756	78.6	673	77.1	59	90.8	324	77.2	349	77.0
Apices	5	0.5	3	0.3	2	3.1	3	0.7	0	0
Bases	0	0	0	0	0	0	0	0	0	0
Petioles	201	20.9	197	22.6	4	6.1	93	22.1	104	23.0

Figure 7.10. Seasonal leaf part selection.

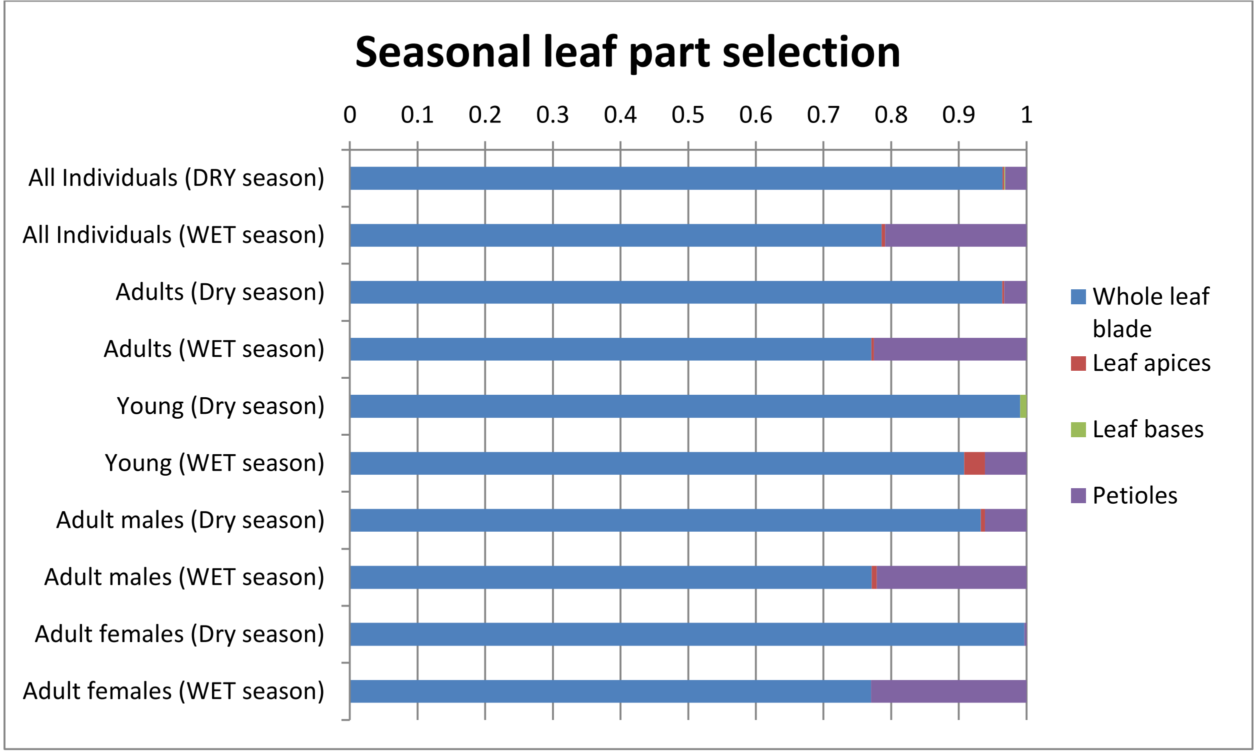


Table 7.7. Significant chi-square results and significant contingency coefficient results.

Section number	Variables compared (Frequency of:)	X^2 results	C-value	Significant
7.3.1.1.	bark selection b/t adult males and females	(1, *N*=2097) = 7.74, p=0.005	0.09	N
7.3.1.2.	young leaf selection b/t adults and young	(1, *N*=1203) = 29.23, p<0.0001	0.22	N
	young leaf selection b/t adult males and females	(1, *N*=1086) = 16.1, p<0.0001	0.17	N
7.3.1.3.	leaf blade selection b/t adults and young	(1, *N*=1683) = 13.89, p=0.0002	0.13	N
	petiole selection b/t adults and young	(1, *N*=1683) = 18.53, p<0.0001	0.15	N
7.3.2.1.	leaf selection b/t wet and dry season in all individuals	(1, *N*=2426) = 7.52, p=0.006	0.08	N
	flower selection b/t wet and dry season in all individuals	(1, *N*=2426) = 35.4, p<0.0001	0.17	N
	bark selection b/t wet and dry season in all individuals	(1, *N*=2426) = 5.64, p=0.02	0.07	N
	leaf selection b/t wet and dry season in adult males	(1, *N*=1011) = 12.28, p=0.0005	0.15	N

	flower selection b/t wet and dry season in adult males	(1, *N*=1011) = 21.12, p<0.0001	0.20	N
	bark selection b/t wet and dry season in adult males	(1, *N*=1011) = 6.78, p=0.009	0.12	N
	leaf selection b/t wet and dry season in adult females	(1, *N*=1086) = 4.76, p=0.03	0.09	N
	flower selection b/t wet and dry season in adult females	(1, *N*=1086) = 18.83, p<0.0001	0.18	N
	bark selection b/t adult males and females in dry season	(1, *N*=856) = 6.7, p=0.01	0.12	N
7.3.2.2.	young leaf selection b/t wet and dry seasons in all individuals	(1, *N*=1230) = 8.11, p=0.004	0.11	N
	young leaf selection b/t wet and dry seasons in all adults	(1, *N*=1086) = 8.29, p=0.004	0.12	N
	young leaf selection b/t wet and dry seasons in adult females	(1, *N*=1011) = 6.78, p=0.009	0.12	N
	young leaf selection b/t adults and young in dry season	(1, *N*=302) = 10.69, p=0.001	0.12	N
	young leaf selection b/t adults and young in wet season	(1, *N*=901) = 13.63, p=0.0002	0.17	N
	young leaf selection b/t adult males and females in dry season	(1, *N*=250) = 18.23, p<0.0001	0.37	Significant
	young leaf selection b/t adult males and females in wet season	(1, *N*=836) = 6.03, p=0.01	0.12	N
7.3.2.3.	leaf blade selection b/t wet and dry season in all individual	(1, *N*=1723) = 114.45, p<0.0001	0.35	Significant
	leaf blade selection b/t wet and dry season in adults	(1, *N*=1512) = 107.89, p<0.0001	0.36	Significant
	leaf blade selection b/t wet and dry season in young	(1, *N*=171) = 5.1, p=0.02	0.24	N
	leaf blade selection b/t wet and dry season in adult males	(1, *N*=746) = 34.57, p<0.0001	0.30	Significant
	leaf blade selection b/t wet and dry season in adult female	(1, *N*=766) = 78.3, p<0.0001	0.43	Significant
	petiole selection b/t wet and dry season in all individuals	(1, *N*=1723) = 116.22, p<0.0001	0.36	Significant
	petiole selection b/t wet and dry season in adults	(1, *N*=1512) = 109.58, p<0.0001	0.37	Significant
	petiole selection b/t wet and dry season in young	(1, *N*=171) = 4.26, p=0.04	0.22	N

	petiole selection b/t wet and dry season in adult males	(1, *N*=746) = 35.36, p<0.0001	0.30	Significant
	petiole selection b/t wet and dry season in adult females	(1, *N*=766) = 78.3, p<0.0001	0.43	Significant
	leaf blade selection b/t adults and young in the wet season	(1, *N*=938) = 5.83, p=0.02	0.11	N
	leaf apex selection b/t adults and young in the wet season	(1, *N*=938) = 4.15, p=0.04	0.09	N
	petiole selection b/t adults and young in the wet season	(1, *N*=938) = 8.73, p=0.003	0.14	N
	leaf blade selection b/t adult males and females in the dry season	(1, *N*=639) = 17.21, p<0.0001	0.23	N

7.3.3. Monthly results

7.3.3.1. Food categories

Monthly variation in food category selection in all individuals is illustrated in Figure 7.11 and Table 7.8. Bark/pith is not included because it was only selected by adult males, selected in low percentages, and only during April, May and July, peaking in May at 4.8% of the diet. Flowers were selected in April and July, although most “unidentified” feeding records during the month of May were most likely flowers. Flowers accounted for 40% of the diet in April. Fruit and seed selection peaked between May and September, ranging from zero percent of the diet in January and October to 54.9% of the diet in September. Leaf selection dominated all months except September, ranging from a low of 45.1% in September to 100% in January and October.

Figure 7.12, Figure 7.13 and Table 7.8 shows monthly variation in food category selection in adult males and adult females. In adult males, bark/pith selection peaked in May at 10.2% of the total diet, and fruit and seed selection peaked in September at 78.4% of the diet. Leaf selection dominates all months except for August and September. For adult females, fruit and seed selection peaked in May at 75.6% of their diet and leaves dominated their diet in all months except May, July and September.

Fruit and seed selection were not correlated with weather, phenology, variation in the use of home range, or the degree of unit cohesion. No graphs or correlation values are shown here. It is not possible to correlate fruit and seed selection with feeding tree fruiting phenology as noted above. It is also not possible to correlate fruit and seed selection with *P. stellata* fruiting because fruiting was not recorded in the dipterocarp trees as noted in Chapter 4. The selection of fruits and seeds are not correlated to their availability.

No correlation analyses were conducted for flowers and bark/pith selection with phenology or weather variables because these food items were only selected during a few months. However, flower selection coincides with peaks in flower availability, and specifically with peaks in *P. stellata* flowering. *P. stellata* trees were only observed to flower during a few months as well, including the months in which flower selection occurred. For adult males, bark/pith selection coincides with flowering peaks. During all adult male bark/pith feeding observations, the adult male removed a branch and carried it with him for up to 35 m while feeding from it before dropping the branch. The selection of young leaves is correlated to phenology in the following subsection.

Table 7.8. Monthly food category budgets.

Month	Food category	All individuals		Adult males		Adult females		Unidentified individuals	
		N	%	N	%	N	%	N	%
January	Fr/s	0	0	0	0	0	0	0	0
	Flowers	0	0	0	0	0	0	0	0
	Leaves	71	100	39	100	28	100	3	100
	B/p	0	0	0	0	0	0	0	0
February	Fr/s	28	4.9	17	7.0	11	4.5	0	0
	Flowers	0	0	0	0	0	0	0	0
	Leaves	541	95.1	225	93.0	233	95.5	14	100
	B/p	0	0	0	0	0	0	0	0
March	Fr/s	23	8.6	7	10.8	7	7.1	9	69.2
	Flowers	0	0	0	0	0	0	0	0
	Leaves	246	91.4	58	89.2	92	92.9	4	30.7
	B/p	0	0	0	0	0	0	0	0

April	Fr/s	2	1.9	1	2.1	1	1.8	na	na
	Flowers	36	34.0	16	34.0	20	36.4	na	na
	Leaves	66	62.2	28	59.6	34	61.8	na	na
	B/p	2	1.9	2	4.3	0	0	na	na
May	Fr/s	56	44.4	22	37.3	34	75.6	0	0
	Flowers	0	0	0	0	0	0	0	0
	Leaves	64	50.8	31	52.5	11	24.4	16	100
	B/p	6	4.8	6	10.2	0	0	0	0
June	Fr/s	8	11.4	0	0	0	0	8	100
	Flowers	0	0	0	0	0	0	0	0
	Leaves	62	88.6	53	100	6	100	0	0
	B/p	0	0	0	0	0	0	0	0
July	Fr/s	15	36.6	4	25	11	50	na	na
	Flowers	3	7.3	0	0	3	13.6	na	na
	Leaves	22	53.7	11	68.7	8	36.4	na	na
	B/p	1	2.4	1	6.3	0	0	na	na
August	Fr/s	39	33.1	19	52.8	18	24	2	100
	Flowers	0	0	0	0	0	0	0	0
	Leaves	79	66.9	17	47.2	57	76	0	0
	B/p	0	0	0	0	0	0	0	0
September	Fr/s	67	54.9	29	78.4	38	52.1	0	0
	Flowers	0	0	0	0	0	0	0	0
	Leaves	55	45.1	8	21.6	35	47.9	12	100
	B/p	0	0	0	0	0	0	0	0
October	Fr/s	0	0	0	0	0	0	0	0
	Flowers	0	0	0	0	0	0	0	0
	Leaves	119	100	40	100	71	100	6	100
	B/p	0	0	0	0	0	0	0	0
November	Fr/s	9	1.4	4	1.4	4	1.3	1	100
	Flowers	0	0	0	0	0	0	0	0
	Leaves	646	98.6	292	98.6	303	98.7	0	0
	B/p	0	0	0	0	0	0	0	0
December	Fr/s	1	0.6	0	0	1	1.6	0	0
	Flowers	0	0	0	0	0	0	0	0
	Leaves	159	99.4	81	100	60	98.4	4	100
	B/p	0	0	0	0	0	0	0	0

Figure 7.11. Monthly selection of fruit and seed, flower, and leaves in all individuals.

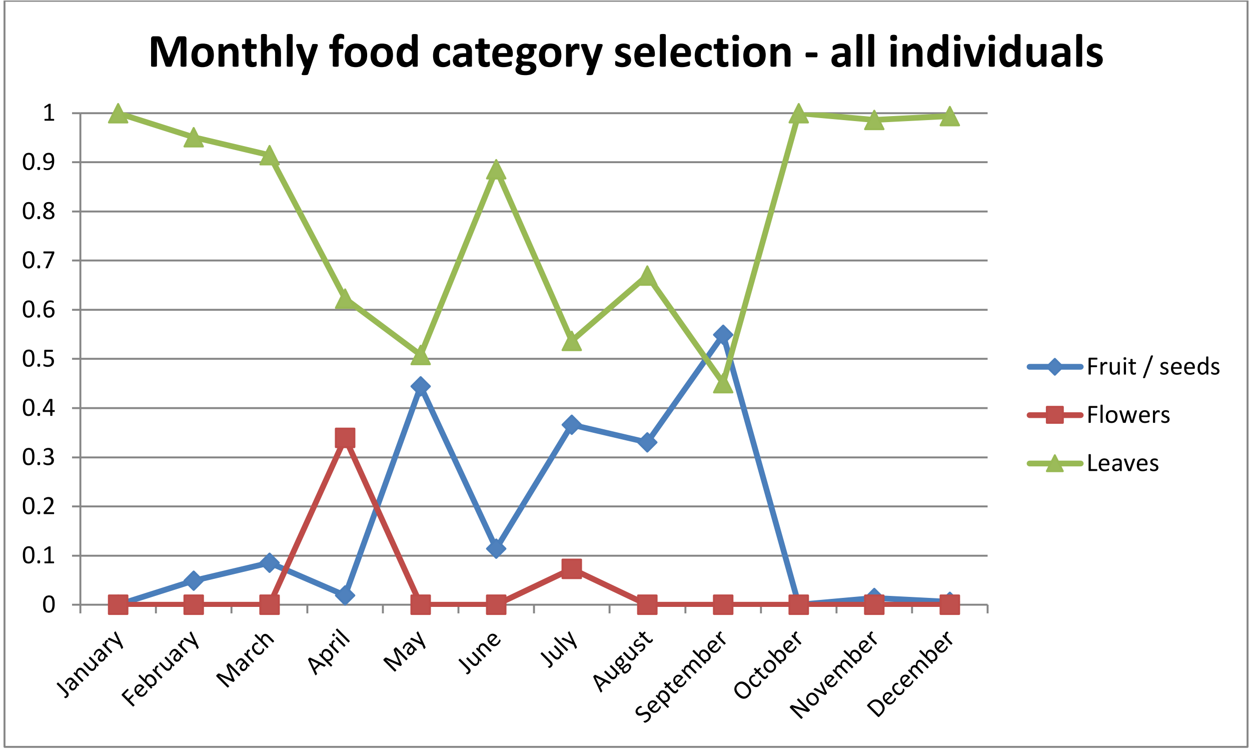


Figure 7.12. Monthly selection of fruit and seed, flower, and leaves in adult males.

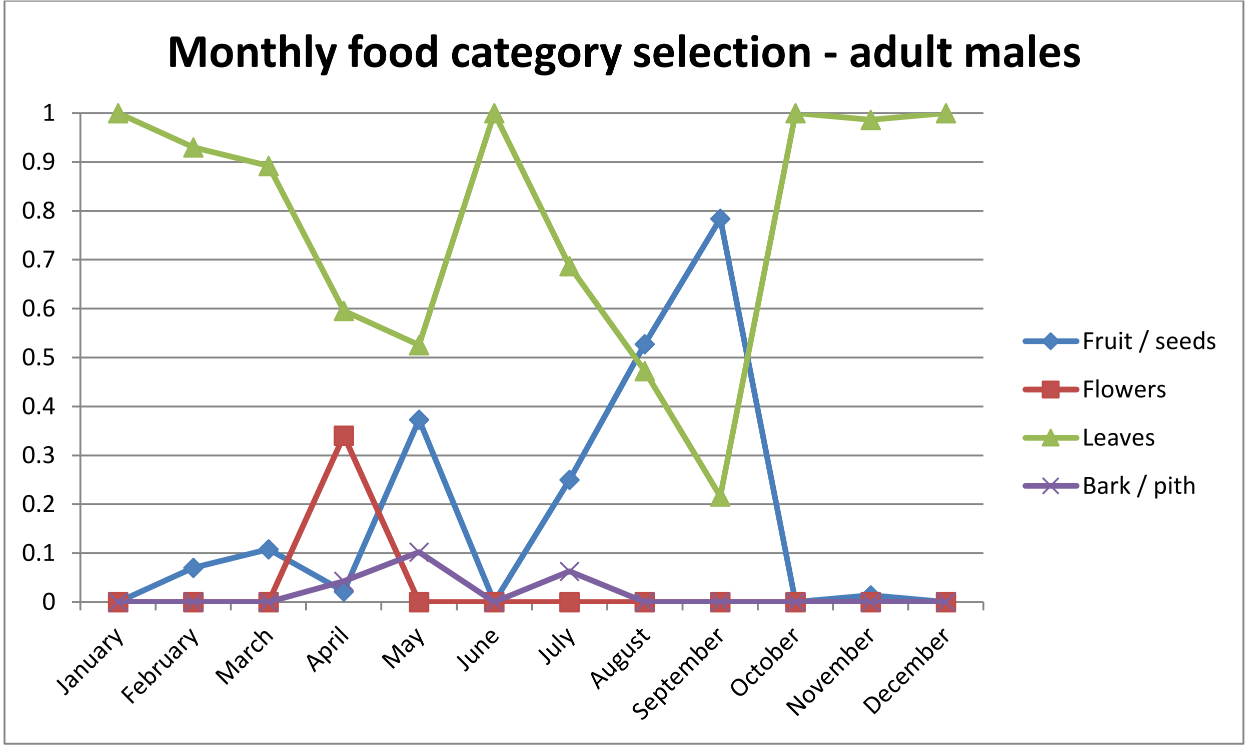
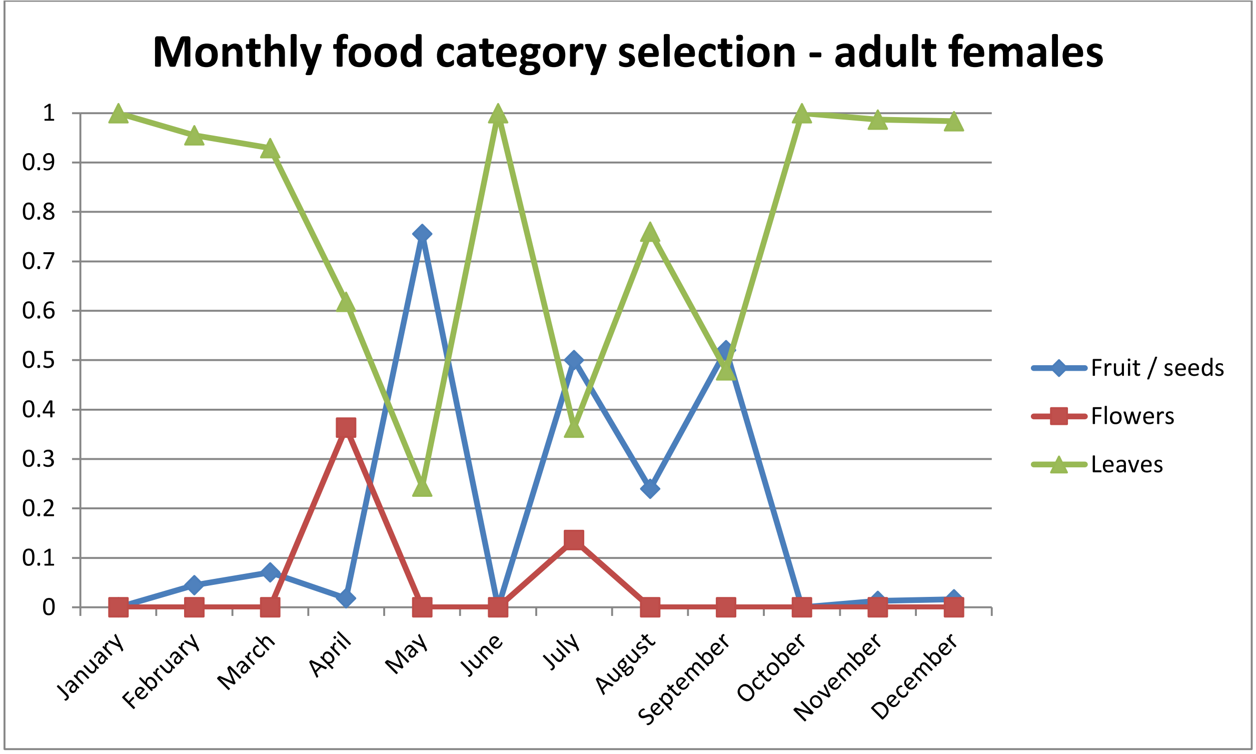


Figure 7.13. Monthly selection of fruit and seed, flower. and leaves in adult females.



7.3.3.2. Leaf age

Monthly variation in the selection of young and mature leaves in all groupings of individuals is illustrated in Figures 7.14 and 7.15, and Table 7.9. As there are only two subcategories, the inverse of young leaf selection represents mature leaf selection.

In all individuals and in all adults there are only two months in which the selection of young leaves drops below 75%: February (59.7%) and November (39.3%). In young individuals, young leaf selection drops below 75% in two different months: June (50%) and July (33.3%). However, this is likely the result of a small sample size during those months (see Table 7.9).

Young leaf selection was not significantly correlated with weather, phenology, variation in the use of home range, or the degree of unit cohesion for all groupings of individuals (all individuals combined, adults, young individuals, adult males or adult females). Young leaf selection was also not significantly correlated to *P. stellata* leaf flush phenology for all groupings of individuals, despite the importance of *P. stellata* to the diet of the doucs (see below). Additional correlations with feeding tree phenology cannot be conducted as noted above. The lack of significant correlations indicates that young leaf selection is not affected by availability. No graphs or correlation values are shown here.

Reduced selection of young leaves in February in adults is entirely attributed to adult males: adult females do not reduce their selection of young leaves during this month. Adult males also reduced young leaf selection in September (25%), which again does not characterize adult females. There are increases in fruit and seed selection in September (Figures 5.12 and 5.13) indicating adult males are not only relying on mature leaves during September. Reduced selection of young leaves in November in all adults does not coincide with increases in fruit and seed, or flower selection (Figures 5.12 and 5.13). In November, petioles of mature leaves form the majority of their diet, although this does not likely reflect dietary stress considering fruits and seeds are most abundant at this time.

Table 7.9. Monthly selection of leaf age.

Month	Food category	All individuals		Adults		Young individuals		Adult males		Adult females	
		N	%	N	%	N	%	N	%	N	%
Jan.	Young	11	100	10	100	1	100	1	100	9	100
	Mature	0	0	0	0	0	0	0	0	0	0
Feb.	Young	80	59.7	62	60.2	18	100	19	33.9	43	91.5
	Mature	54	40.3	41	39.8	0	0	37	66.1	4	8.5
Mar.	Young	67	81.7	39	73.6	25	96.2	17	70.8	22	75.9
	Mature	15	18.3	14	26.4	1	3.8	7	29.2	7	24.1
Ap.	Young	60	93.8	56	93.3	4	100	28	100	28	87.5
	Mature	4	6.2	4	6.7	0	0	0	0	4	12.5
May	Young	32	84.2	29	85.3	3	75.0	19	79.2	10	100
	Mature	6	15.8	5	14.7	1	25.0	5	20.8	0	0
June	Young	47	94.0	46	95.8	1	50.0	40	95.2	6	100
	Mature	3	6.0	2	4.2	1	50.0	2	4.8	0	0
July	Young	13	76.5	12	85.7	1	33.3	9	81.8	3	100
	Mature	4	23.5	2	14.3	2	66.7	2	18.2	0	0
Aug.	Young	77	98.7	73	100	4	80.0	17	100	56	100
	Mature	1	1.3	0	0	1	20.0	0	0	0	0

Sept.	Young	37	84.9	37	86.1	na	na	2	25.0	35	100
	Mature	7	15.9	6	13.9	na	na	6	75.0	0	0
Oct.	Young	106	99.1	98	99.0	2	100	33	97.1	65	100
	Mature	1	0.9	1	1.0	0	0	1	2.9	0	0
Nov.	Young	176	39.3	142	34.6	34	89.5	75	36.8	67	32.5
	Mature	272	60.7	268	65.4	4	10.5	129	63.2	139	67.5
Dec.	Young	138	87.9	120	86.3	14	100	61	76.3	59	100
	Mature	19	12.1	19	13.7	0	0	19	23.7	0	0

Figure 7.14. Monthly selection of young leaves in all individuals, adults, and young individuals.

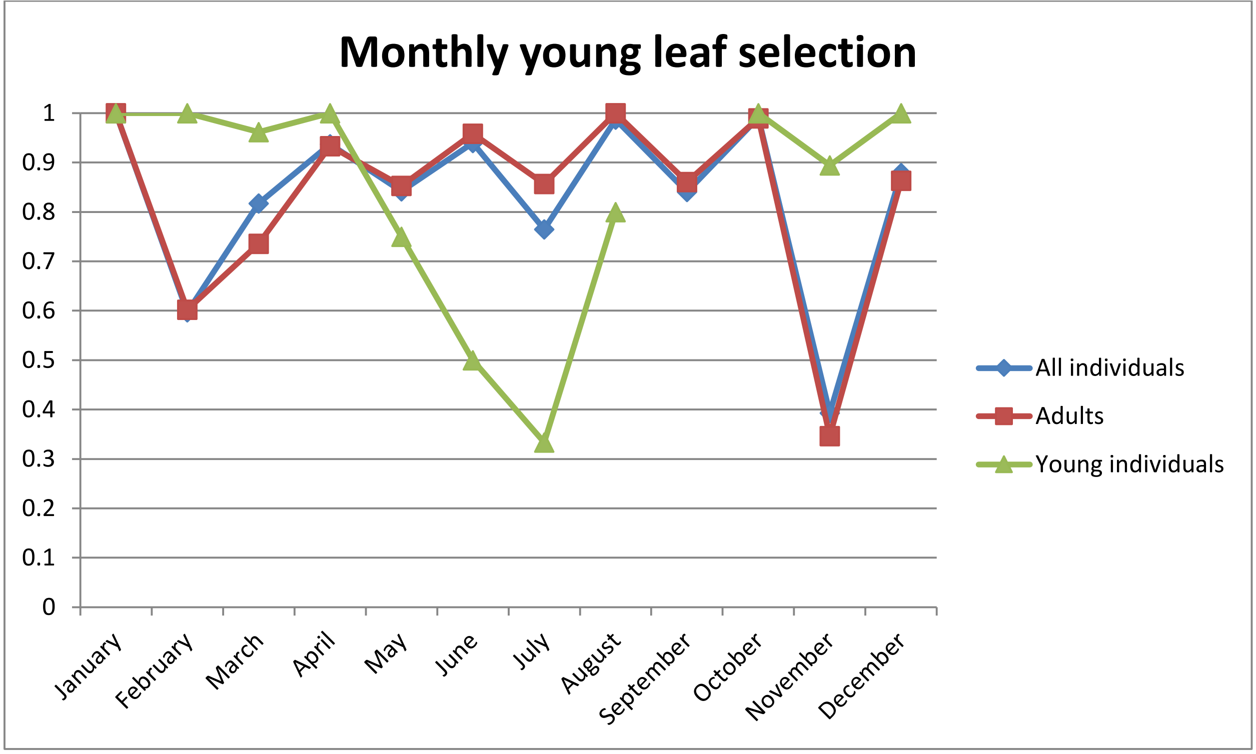
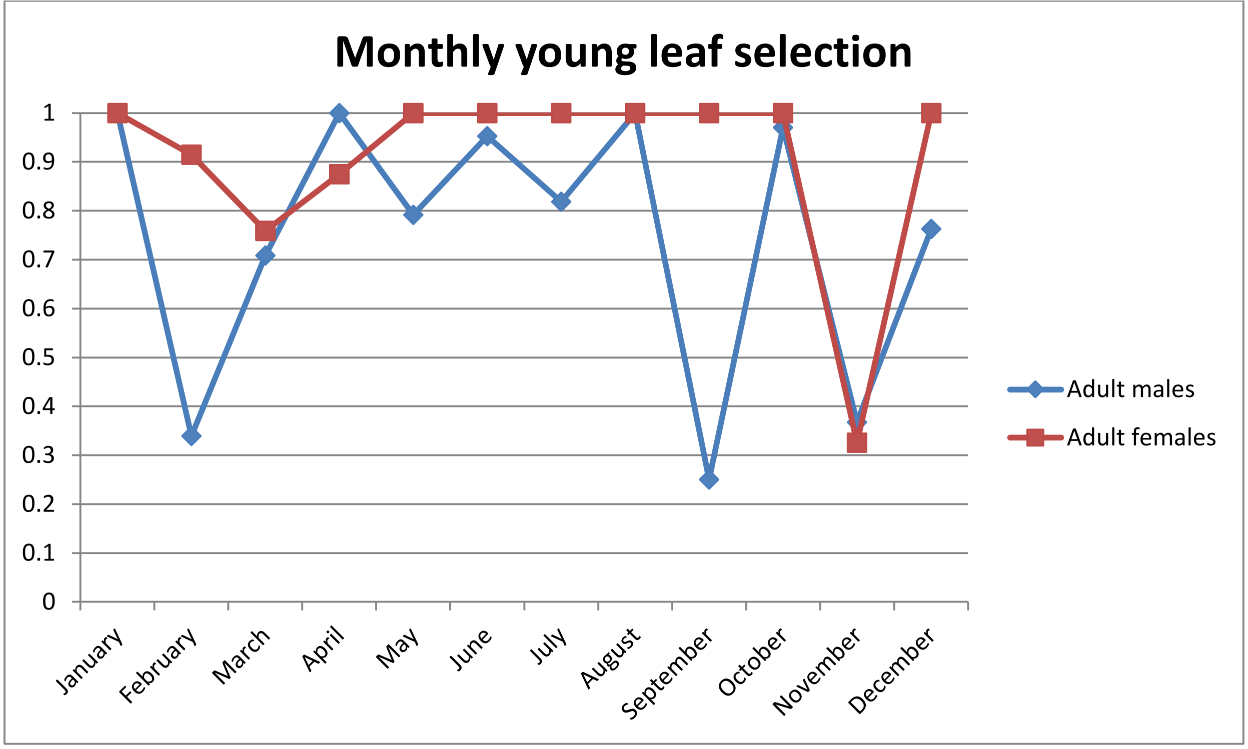


Figure 7.15. Monthly selection of young leaves by adult males and adult females.



7.3.3.2. Leaf parts

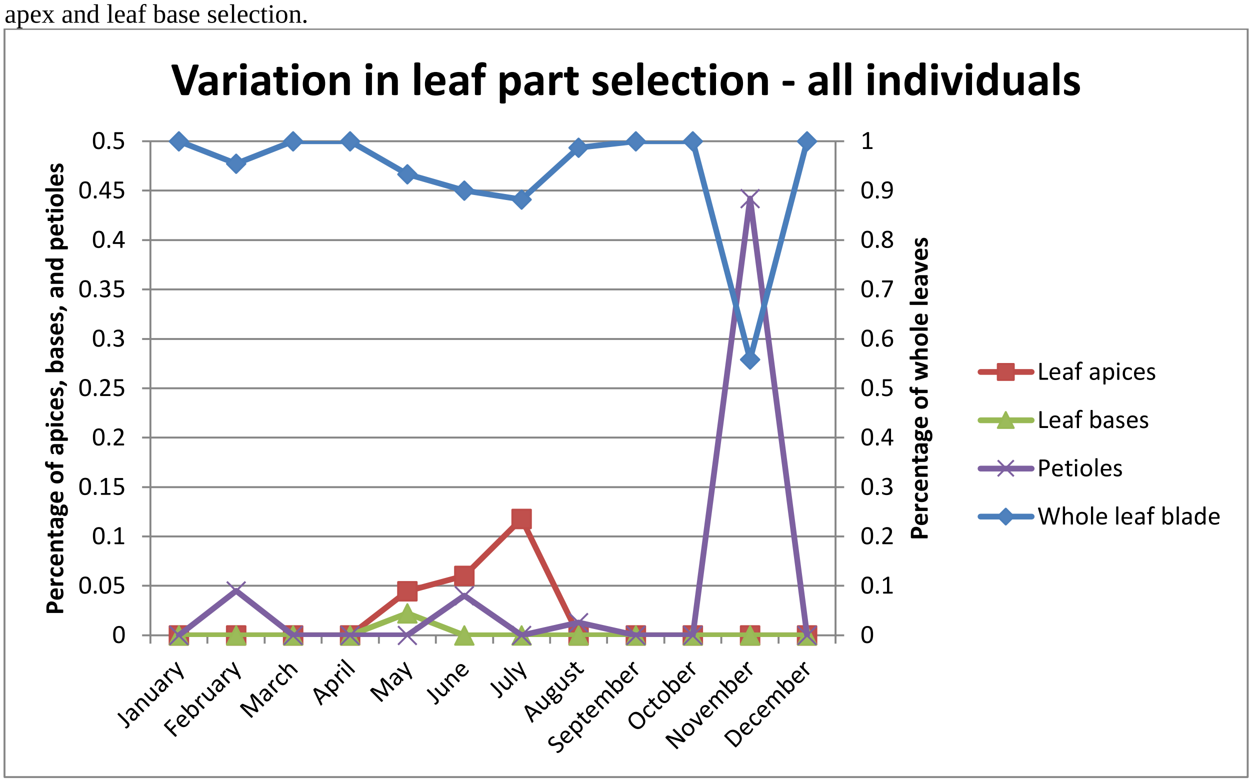
Monthly variation in leaf part selection in all individuals is illustrated in Figure 7.16. This reflects the pattern observed among adults, young individuals, adult males and adult females, which are therefore not illustrated individually. Monthly selection values are not shown in a table because of the low frequency of selection for petioles, apices and bases.

Whole leaf blades were most commonly selected among all groupings of individuals. Among all individuals, whole leaf blade feeding only dropped below 90.0% in two months: July (88.2%) and November (55.8%). Selection for leaf blade apices and bases was rare, but peaked between May and July, being greatest in July at 11.8%. These peaks are entirely attributed to the adult males in May and June (6.9% and 7.1%) and young individuals in July (66.7%). Adult females did not select leaf apices or bases.

Petioles were selected during February, June, August and November. November represents the greatest percentage in petiole selection in all individuals, adult males and adult females (44.2%, 44.6%, and 50.5%). In November, mature leaves accounted for a majority of the diet with the remainder being young leaves. Of those mature leaves, petioles accounted for nearly half of the diet. Petioles cannot be considered a fall-back resource in November, given that fruits and seeds are abundant during that month. Mature leaves are most likely a fall-back resource. Young individuals fed on stems only in August and November. August represented their most significant petiole selection (20%), which is likely the result of sample size.

No statistical analyses were conducted because the selection of petioles, apices and bases was overall rare.

Figure 7.16. Monthly selection of leaf parts in all individuals.
Whole leaf percentages are represented on the secondary vertical axis to provide for readable values in petiole, leaf apex and leaf base selection.



7.3.4. Nursing

Nursing was observed on five separate occasions accounting for nine records. Three of these observations occurred during August, one in September and one in October.

7.3.5. Food species

7.3.5.1 Annual results

All identified foods (N=62) are shown in Table 7.10, including the percentage of selection for food categories and subcategories. The percentage of leaves (and all other categories) for a certain species represents the percentage in which leaves of that species were selected in relation to the selection of leaves in all other species. Results are presented for all individuals, and food species are arranged according to family. Additional notes include their season of selection and whether the food item was selected from a douc group in the wild, the confiscated douc male, or both (see Methods above).

Red-shanked doucs were observed to feed from 79 plant species, of which 62 were identified and 17 remained unidentified. Species diversity is low.

For food categories, 187 of the total 248 fruit and seed feeding observations were identified, all 39 of the flower feeding observations were identified, and 1377 of the 2130 leaf feeding observations were identified. For subcategories, all 225 of the petiole feeding observations were identified, five of the eight leaf apex or base records were identified, and seven of the nine bark/pith feeding observations were identified.

The 62 identified foods represent 28 families. Of these, 54 species (22 families) are flowering tree species or shrubs (87.1%) and eight species (six families) are lianas or epiphytes (12.9%). Lianas and epiphytes accounted for over half of the total leaf feeding observations (53.4%), and for 10.3% of the flower feeding observations. This indicates the importance of these plants to the doucs' diet. Notably, no species was observed to be exploited for fruits and seeds, flowers, and leaves alike. However, 10 species (16.1%) were exploited for at least two of these food categories.

7.3.5.2. Seasonal results

In the dry season, doucs selected 26 different plant species of 17 families, and in the wet season they selected 33 different plant species of 18 families. Only nine species were observed to be selected in both the wet and dry season, indicating seasonal change in dietary species. Species and family diversity are comparable between the two seasons suggesting red-shanked doucs on Son Tra do not adapt to potential seasonal dietary stresses by increasing dietary species diversity. Of the nine food species selected in both seasons, three have significant importance to the diet of doucs on Son Tra, including *P. stellata*, and two epiphyte species: *Parsonsia laevigata* and *Ipomoea eberhardtii*.

7.3.5.3. Food categories and subcategories

Fruits and seeds of 22 species of 11 families were selected (35.5% of food species). Among them, just two species accounted for nearly half of all fruit and seed feeding observations: *Garcinia morella* (30.0%) and *Ficus variegata* (16.0%). The families of these two species (Guttiferae and Moraceae) represent 14 food species and account for 68.4% of all fruit and seed feeding observations: 38.0% from Guttiferae species, and 30.4% from Moraceae species. For dry fruits, the doucs consumed and fractured the seeds, but for fleshy fruits the doucs appear to play a role in seed dispersal.

Flowers of four species of three families were selected (6.5% of food species). Among them *P. stellata* accounted for most feeding observations (82.1%).

Leaves of 46 species of 22 families were selected (74.2% of food species). Among them *P. stellata* was the most commonly selected (36.3%), followed by *P. laevigata* (18.7%) and *I. eberhardtii* (18.7%). *I. eberhardtii* grows primarily along roadsides due to disturbance. It is considered an invasive species on Son Tra and the city administration puts considerable efforts towards its eradiation (China Daily, 2004; Department of Agriculture and Rural Development, personal communication, 2013). These three families accounted for 74.9% of all leave feeding observations.

Petioles were selected in four species of four families (6.5% of food species). Among them *Ancistrocladus tectorius* accounted for most petiole feeding observations (75.6%). The remainder is largely attributed to *Ficus depressa* (23.1%).

Selection for leaf blade apices or bases occurred in two species of two families including *P. stellata* (60%) and *Helicteres angustifolia* var. *obtusa* (40%).

Bark/pith was selected in two species of two families including *P. stellata* (85.7%) and *F. depressa* (14.3%).

7.3.5.4. Food species diversity and selectivity

There are 1022 plants species currently identified for Son Tra (Chapter 3 and Appendix 6). The doucs selected foods from between 62 and 79 species, therefore their dietary diversity is between 6.1% and of 7.7%. This indicates a low dietary diversity, and highlights the importance of the identified food species to the doucs survival on Son Tra.

Along transects, the four most abundant tree families accounted for 46.7% of all transect trees: Euphorbiaceae (17.4%), Myrtaceae (11.3%), Dipterocarpaceae (9.6%), and Sapindaceae (8.4%). Comparatively, the doucs only selected leaves from Euporbiaceae, Myrtaceae and Sapindaceae, and leaf selection from these three families combined accounted for only 3.5% of all leaf feeding observations. In contrast, dipterocarp leaves were the most commonly selected leaf food (36.3%), in addition to their flowers (82.1%) and bark/pith (85.7%), and therefore one of the dominant families on Son Tra also dominates the diet of the doucs. Of the 28 food families, Moraceae contained the most number of food species (n=12 species or 19.4%), followed by Myrtaceae (n=six species or 9.7%). Myrtaceae is an abundant family on Son Tra but Moraceae is not, indicating the selectivity of Moraceae.

These data suggest the doucs are selective feeders. Specifically, and as shown in sections 7.3.3.1 and 7.3.3.2 above, phenology data (Chapter 4) for fruiting and leaf flush were not significantly correlated with selection. These resources are selected irrespective of their availability. Given that flowers and bark were only selected in a few months, it is not appropriate to conduct correlation analyses. However, the selection of flowers and bark both peak with the primary peak in flowering.

Several species emerge as very important to the diet of the red-shanked douc on Son Tra Nature Reserve: *Parashorea stellata*, *Parsonsia laevigata*, *Ipomoea eberhardtii*, *Ancistrocladus tectorius*, Guttiferae species (n=2) and Moraceae species (n=12).

Table 7.10. Food species list.

Percentage values are relative to their category/subcategory. Fr/s=fruits and seeds, Fl=flowers, L=leaves, St=stems, A/b=leaf apices or bases, and B/p=bark/pith. List includes foods from wild groups (W), foods selected by the confiscated douc (C), and foods from wild groups after data collection ended (Aft). For “C” and “Aft” the food categories selected for are denoted with an X. Sn=season the species was observed to be selected during, including the dry season (D) and wet season (W).

Family	Species		Fr/s	Fl	L	St	A/b	B/p	List	Sn
Anacardiaceae	*Semecarpus reticulata* Lec.	N			6				W	D W
		%			0.4					
Ancistrocladaceae	*Ancistrocladus tectorius* (Lour.) Merr.	N			204	170			W	D
		%			14.8	75.6				
Apocynaceae	*Cleghornia malaccensis* (Hook.f.) King et Gamble	N			17				W	W
		%			1.2					
	Parsonsia laevigata (Moon) Alston	N			258				W	D W
		%			18.7					
Araliaceae	*Schefflera quangtriensis* Shang.				X				C	

Combretaceae	*Quisqualis indica* L. var. *pierrei* (Gagnep.) O. Lecompte				X				Aft	W
Convolvulaceae	*Aniseia harmandii* (Gagnep.) Phamhoang				X				C	
	Ipomoea eberhardtii Gagnep.	N			258				W	D W
		%			18.7					
Dipterocarpaceae	*Parashorea stellata* Kurz.	N		32	500	2	3	6	W	D W
		%		82.1	36.3	0.9	60.0	85.7		
Euphorbiaceae	*Claoxylon indicum* (Reinw. ex Blume) Hassk.		X		X				C	
	Glochidion velutinum Wight.		X		X				C	
	Mallotus floribundus (Bl.) Muell.-Arg..	N			19				W	D
		%			1.4				C	
	Flueggea jullienii (Beille) G.L.Webster				X				C	
Fabaceae	*Archidendron chevalieri* (Kosterm.) I.C. Nielsen	N	2						W	W
		%	1.1							
Fagaceae	*Lithocarpus annamitorus* (A. Chev.) A. Camus	N			2				W C	D W
		%			0.2					
	Lithocarpus fenestratus (Roxb.) Rehder	N	24						W	W
		%	12.8							
	Lithocarpus gigantophyllus (Hickel & A.Campus) A. Camus	N	8						W	W
		%	4.4							
	Lithocarpus thomsonii (Miq.) Rehder	N	1						W	W
		%	0.5							
Flacourtiaceae	*Flacourtia montana* Graham	N	1						W	W
		%	0.5						C	
Guttiferae	*Garcinia morella* (Gaertn.) Desr.	N	56						W	W
		%	30.0							
	Garcinia oligantha Merr.	N	15						W	W
		%	8.0							
Lauraceae	*Cinnamomum durifolium* Kosterm.	N			1				W	D
		%			0.1					
	Dehaasia caesia Bl.	N	4	3					W	D W
		%	2.1	7.7						
	Litsea glutinosa (Lour.) C. Rob.			X	X				C	
	Litsea salmonea A. Chev.				X				C	
	Litsea umbellata (Lour.) Merr.				X				C	
Loganiaceae	*Strychnos dinhensis* Pierre ex Dop.	N			6				W	D
		%			0.4					
Malpighiaceae	*Aspidopterys tomentosa*	N			2				W	W

	(Bl.) A.Juss.	%			0.2					
Meliaceae	*Dysoxylum cauliflorum* Hiern.	N	19						W	D
		%	10.2							
	Dysoxylum cyrtobotryum Miq.	N			1				W	W
		%			0.1					
	cf. Dysoxylum samoense A. Gray	N			3				W	D
		%			0.2					
	Trichilia connaroides (Wight & Arnott) Bentvelzen	N			2				W	D
		%			0.2					
Moraceae	*Ficus auriculata* Lour.	N			4				W	D
		%			0.3					
	Ficus callophylla Bl.		X						Aft	W
	cf. Ficus costata Aiton	N	2						W	W
		%	1.1							
	Ficus curtipes Corner	N			1				W	W
		%			0.1					
	Ficus depressa Bl.	N	10		2	52		1	W C	D W
		%	5.3		0.2	23.1		14.3		
	Ficus lamponga Miq.				X				C	
	Ficus nervosa Heyne ex Roth.				X				C	
	Ficus sagittata Vahl		X						Aft	W
	Ficus sarmentosa Buch.-Ham. ex Sm. var. *nipponica* (Franch. & Sav.) Corner	N	2		6				W	D
		%	1.1		0.4					
	Ficus subcordata Bl.	N	9		39				W	D
		%	4.8		2.8					
	cf. Ficus trichocarpa Bl. var. *obtusa* (Hasskarl) Corner	N	4		8				W	D W
		%	2.1		0.6					
	cf. Ficus variegata Bl.	N	30						W	D W
		%	16.0							
Myrtaceae	*Decaspermum gracilentum* (Hance) Merr. & Perry	N			5				W C	W
		%			0.4					
	Decaspermum humile (G.Don) A.J. Scott	N			2				W	W
		%			0.2					
	Syzygium cumini (L.) Skeels	N			5				W C	W
		%			0.4					
	Syzygium lineatum (Bl.) Merr. & Perry	N			1				W	D
		%			0.1					
	Syzygium polyanthum (Wight) Walp.	N			2				W	D
		%			0.2					
	cf. Syzygium	N			6				W	W

	stictanthum Merr. & L.M.Perry	%			0.4					
Phyllanthaceae	*Baccaurea silvestris* Lour.		X						Aft	W
Rutaceae	*Macclurodendron oligophlebia* (Merr.) Hartl.		X		X				C	
	Zanthoxylum avicenae (Lam.) *DC.*	N			2				W	D
		%			0.2					
Sapindaceae	*Amesiodendron chinense* (Merr.) Hu	N			1				W	D
		%			0.1					
	Paranephelium spirei Lecomte	N			7				W	W
		%			0.5					
Sapotaceae	*Palaquium annamense* Lecomte				X				C	
Sterculiaceae	*cf. Helicteres angustifolia* L. var. *obtusa* Pierre	N			4	1	2		W	D W
		%			0.3	0.4	40.0			
Styracaceae	*Styrax benjoin* Dryand.				X				C	
Theaceae	*Eurya japonica* Thunb.		X						C	
Tiliaceae	*Grewia bulot* Gagnep.	N			2				W	D
		%			0.2					
Verbenaceae	*Vitex leptobotrys* Hallier	N			1				W	W
		%			0.1					
Vitaceae	*cf. Tetrastigma touranense* Gagnep.	N		4					W	D
		%		10.3						
TOTALS			187	39	1377	225	5	7		

7.3.6. Chemical and nutritional analyses

Twenty-two samples of 12 species and 10 families were tested, consisting of 15 leaf samples, five fruit and seed samples, one flower sample, and one bark/pith sample (Table 7.11). Petioles were not tested because it would have required the complete defoliation of *Ancistrocladus tectorius* trees. Due to the small sample size, comparisons are mostly descriptive.

Water, ash, tannin, crude protein, NDF and ADF contents for the individual samples by food category are shown in Tables 7.11 and 7.12.

Four samples represent plant species or parts that were not consumed by the doucs during the time of observation to test for differences between selected and non-selected foods. For leaves, 12 samples were of selected leaves and three were of non-selected leaves. Of the selected leaves, seven samples were of young leaves, three were mature leaves, and two samples combined both young and mature leaves. All non-selected leaf samples were of combined young and mature leaves. For fruit, four samples represent selected fruit and one represents a pericarp (shell) that was discarded during seed consumption.

Combining all tested samples, mature leaves contained slightly more water (4.40 ± 3.22) than young leaves (3.95 ± 1.44). Water content was lowest in the flower sample (1.83). Dry matter (ash) was greatest in mature leaves (10.69 ± 5.95), followed by young leaves (6.54 ± 2.28). Fruits and seeds had the least dry matter (3.43 ± 2.4). Tannin content was highest in the flower sample (19.4), followed by young leaves (11.50 ± 9.32). Fruits and seeds contained the least tannins (3.19 ± 1.35). Crude protein was greatest in mature leaves (12.63 ± 2.64), followed by flowers (11.19) and young leaves (11.18 ± 4.73). The bark/pith sample contained the most NDF (64.6), followed by young leaves (57.8 ± 9.7), fruit and seeds (56.26 ± 16.99), mature leaves (49.7 ± 3.44) and flowers (27.1). This same pattern was found for ADF.

Protein-to-fiber ratios of selected young leaves was lower (0.2 ± 0.1) than selected mature leaves (0.26 ± 0.07), although the difference was minimal and suggests that mature leaves and young leaves are nutritionally comparable from a protein-to-fiber perspective. Results of the unpaired student's *t*-tests revealed no significant differences in water, ash, tannin, crude protein, NDF, and ADF between selected mature and selected young leaves. This means selected mature leaves were of comparatively high quality.

Protein-to-fiber ratios of selected leaves were higher (0.21 ± 0.1) than non-selected leaves (0.15 ± 0.02) suggesting selected leaves are higher quality than non-selected leaves. Results of the unpaired student's *t*-tests revealed no significant differences in water, ash, tannin, crude protein, NDF, and ADF between selected and non-selected leaves. Leaf selection may not be influenced by the nutrients tested in this study, despite descriptive differences.

P. stellata is a significant keystone resource for the doucs on Son Tra, the doucs regularly exploited this food, and this species was tested several times. Comparing *P. stellata* nutritional quality to the quality of other tested leaves allows for a comparison between a frequently selected food and less frequently selected foods. Young and mature *P. stellata* leaf samples were compared to other selected leaf samples. Protein-to-fiber ratios of *P. stellata* leaves (0.22 ± 0.07) was similar to other selected leaves (0.23 ± 0.1) and results of the unpaired student's *t*-tests revealed no significant differences in water, ash, tannin, crude protein, NDF, and ADF.

Table 7.11. Chemical and nutritional content according to food categories and selection.
All=all leaves including selected and non-selected leaves, Fr/s=fruits and seeds, Fl=flowers, B/p=bark/pith, YL=young leaves, ML= mature leaves, SL= selected leaves, NSL=non-selected leaves, P.sL=*P. stellata* leaves, and O L=selected leaves of non *P. stellata* species.

Element analysis		All	Fr/s	Fl	B/p	YL	ML	SL	NSL	P.s L	O L
	N	15	5	1	1	7	3	12	3	5	7
Water (ml/g)	Avg.	3.58	2.76	1.83	2.14	3.95	4.40	3.86	2.55	2.61	4.91
	SD	1.95	0.64			1.44	3.22	2.08	0.69	0.89	2.21
Ash %	Avg.	7.22	3.434	5.87	3.56	6.54	10.69	7.70	5.33	6.08	8.85
	SD	3.66	2.40			2.28	5.95	3.87	1.62	1.18	4.63
Tannin %	Avg.	8.84	3.19	19.4	5.09	11.50	6.79	10.30	2.99	15.40	6.65
	SD	7.73	1.35			9.32	5.21	7.92	2.42	8.13	5.32
Crude protein %	Avg.	11.16	5.578	11.19	4.06	11.18	12.63	11.64	9.25	10.91	12.16
	SD	3.70	0.46			4.73	2.64	3.92	1.58	3.27	4.24
NDF %	Avg.	55.91	56.26	27.1	64.60	57.80	49.70	53.93	63.83	48.76	57.61
	SD	9.59	16.99			9.70	3.44	9.19	6.57	4.20	9.98
ADF %	Avg.	49.24	46.3	25.9	55.60	49.59	43.43	47.26	57.17	40.76	51.90
	SD	11.79	17.71			15.20	3.40	12.26	3.81	9.80	11.73
Protein : Fiber	Avg.					0.20	0.26	0.21	0.15	0.22	0.23
	SD					0.10	0.70	0.10	0.02	0.07	0.10

Table 7.12. Chemical and nutritional content according to plant sample.

Part tested includes Fr/s=fruits and seeds, Fl=flowers, B/p=bark/pith, YL=young leaves, and ML= mature leaves. Season of the feeding observation is noted (Sn). Group of individuals observed to eat the food (Gp) include adults=Ad, young individuals=Y, adult males=AM, and adult females=AF.

Species	Part tested	Sn	Gp	Element analysis					
				Water (ml / g)	Ash %	Tannin %	Crude protein %	NDF %	ADF %
P. stellata	B	Dry	AM	2.14	3.56	5.09	4.06	64.6	55.6
P. stellata	ML	Dry	AM	2.16	7.08	6.18	11.89	54.1	48.1
P. stellata	ML	Wet	Ad & Y	2.08	5.92	13.46	9.83	49.3	42.1
P. stellata	YL	Wet	Ad & Y	2.24	3.91	28.86	5.98	42.3	40.8
P. stellata	YL & ML	Wet	AM & AF	2.17	7.14	8.85	10.72	52.0	50.3
P. stellata	YL	Wet	Ad & Y	4.38	6.37	19.64	16.12	46.1	22.5
P. stellata	FL	Dry	Ad & Y	1.83	5.87	19.4	11.19	27.1	25.9
P. laevigata	YL	Wet	Ad & Y	3.87	5.46	1.82	10.99	65.3	60.2
F. subcordata	YL	Dry	Ad & Y	6.54	11.79	4.61	19.88	54.5	37.1
F. subcordata	YL	Wet	AF	2.36	5.76	9.46	6.61	70.5	68.2
F. curtipes	YL	Wet	Ad & Y	4.32	6.27	2.06	10.25	63.2	57.1
H. angustifolia	ML	Wet	Y	8.95	19.08	0.73	16.16	45.7	40.1
S. cumini	YL & ML	Wet	Ad	3.39	7.37	13.82	12.83	41.4	39.4
D. cauliflorum	Fr /s	Dry	Ad & Y	2.79	2.54	3.52	6.2	28.4	12.0
F. montana	Fr /s	Dry	Ad & Y	3.65	3.38	2.61	5.9	51.4	48.0
L. annamitorus	YL	Wet	Ad	NA	6.21	14.07	8.42	62.7	61.2
L. gigantophylla	Fr / s	Wet	Ad & Y	2.51	1.27	1.33	5.68	76.9	56.1
L. gigantophylla	Fr / s (seed shells)	Wet	No	1.73	1.96	3.03	4.94	70.8	61.8
L. gigantophylla	YL & ML	Wet	No	1.87	3.20	2.06	7.72	67.5	60.8
D. caesia	YL & ML	Wet	No	3.49	7.11	0.61	11.42	69.4	58.8

G. oligantha	YL & ML	Wet	No	2.3	5.68	6.31	8.60	54.6	51.9
G. oligantha	Fr / s	Wet	Ad & Y	3.12	8.02	5.46	5.17	53.8	53.6

7.4. Discussion

7.4.1. Annual feeding variation and comparisons

The diet of the red-shanked doucs on Son Tra is dominated by leaves (87%), and young leaves were selected most frequently (68.6% of leaf selection). This is comparable to Lippold (1998) who reported *Pygathrix* was predominantly folivorous (82% leaves).

Other *Pygathrix* studies reported that leaves were a common but less dominant dietary item. Rawson (2009) reported 40% leaf feeding in black-shanked doucs, Hoang Minh Duc (2007) reported 54% leaf feeding in black-shanked doucs, Ha Thang Long (2009) reported 59% leaf feeding in grey-shanked doucs, and Phiapalath et al. (2011) estimated about 59% leaf feeding in red-shanked doucs.

The percentage of leaf feeding observed in this study is relatively high compared to Asian colobines, and generally more comparable to African colobines (Chapter 2, Table 2.7 and 2.8). For Asian colobines, the Delacour's langur (*Trachypithecus delacouri*) in Van Long Nature Reserve, Vietnam had a similar feeding budget (Workman, 2010a; 2010b). In African colobines, *Colobus guereza* had a similar feeding budget (Chapman et al., 2004; Wasserman & Chapman, 2003). Yet, various studies on *C. guereza* populations reported remarkably different feeding budgets (Chapter 2), even within the same population. This highlights the problems in characterizing a single species or a single population by a single feeding budget. One potential reason for the high degree of folivory on Son Tra might be the high degree of evergreen trees which contain between 1% and 25% young leaves throughout the year (Chapter 4), and the comparatively high quality of selected mature leaves. This is similar to the Delacour's langurs in northern Vietnam. This may also relate to the degree of habitat disturbance on Son Tra, and the loss of certain tree species previously selected for their flowers, fruits or seeds.

7.4.2. Seasonal and monthly feeding variation and comparisons

Adult females select young leaves significantly more than adult males in the dry season. This might suggest that males select “lower quality” food items (mature leaves and bark) compared to females. However, chemically and nutritionally analyses suggests mature and young leaves are of comparable quality and there is no difference in quality of items chosen by adult males, adult females, and young individuals. The selection of younger leaves might have a chemical or nutritional influence beyond the contents tested in this study. The selection of bark by adult males in the dry season accounts partly for the significant difference, and appeared to be a form of display rather than consumption of food for nutritional value. As shown in Chapter 6, males significantly increase display behavior during peaks in leaf flush.

Young leaf consumption did not correlate with leaf flush phenology. There was no seasonal difference in the selection of fruits and seeds, and their selection also did not correlate with availability. This indicates that young leaves, and fruit and seeds, are dietary staples. This also suggests the doucs are selective feeders, given they select these items irrespective of availability. In contrast, flower, and bark/pith consumption increased during peaks in flowering. Petiole selection was significantly more frequent in the wet season (peaking in November), and therefore whole leaf blade selection was significantly more frequent in the dry season.

This seasonal pattern is different from the pattern reported by Hoang Minh Duc (2007) for which leaf selection in black-shanked doucs increased during the dry season, and fruit and seed selection increased in the wet season. Rawson (2009) reported a similar pattern although results were not significant. Ha Thang Long (2009) reported that young leaf selection and availability significantly and positively correlated in grey-shanked doucs. In this study, the lack of correlation between leaf selection and availability, and fruit/seed selection and availability, might relate to the availability of these foods throughout the year on Son Tra (Chapter 4).

As noted by van Schaik et al. (1993), dietary seasonality is not the only response to fluctuations in the availability of preferred foods. Seasonal breeding and seasonal movements may also be responses to dietary stress. Ranging behaviors were not correlated to food selection in this study, and it appears that dietary stress on Son Tra is minimal. However, moving comprising a relatively high percentage of the activity budget (Chapter 6), and this appears to relate to the reduction of dietary stresses (scramble competition).

7.4.3. Food species and selectivity

Combining all *Pygathrix* studies, the range of plant families of foods identified in *Pygathrix* studies illustrates a great dietary diversity.

Hoang Minh Duc (2007) identified six important food plant families for black-shanked doucs in Vietnam including Fabaceae, Annonaceae, Irvingiaceae, Burseraceae, Myrtaceae, and Dipterocarpaceae. This compares well with the six plant families which Rawson (2009) reported to be the main food sources for black-shanked doucs in Cambodia, including Fabaceae, Myrtaceae, Irvingiaceae, Combretaceae, Lythraceae, and Dipterocarpaceae.

Among those families, only Myrtaceae was identified as an important food plant family for grey-shanked doucs reported by Ha Thang Long (2009), who found Sapindaceae, Theaceae, Myrtaceae, Fagaceae, Polygalaceae and Moraceae were the most important families. Nguyen Thi Tinh et al. (2012) reported on the same population of grey-shanked doucs as Ha Thang Long, and with the same study groups, but noted different important food families including Sapindaceae, Myrtaceae, Guttiferaceae, Burseraceae, and Loganiaceae. Finally, Phiapalath

(2009) noted the six important families for red-shanked doucs in Laos as Sapindaceae, Fagaceae, Meliaceae, Moraceae, Ebenanceae, and Euphorbiaceae.

In this study, the six most important food plant families were Dipterocarpaceae, Apocynaceae, Convolvulaceae, Guttiferae, Moraceae, and Ancistrocladaceae, sharing the most overlap with those identified for grey-shanked doucs in Kon Ka Kinh National Park.

The two grey-shanked douc studies occurred on the same groups in the same study site, and both were long-term studies. Of interest, they share only two of their top five important families. This shows that even among the same groups, feeding habits appear to vary temporally. This may also be related to sampling biases. Chapman & Chapman (1999) noted that small scale habitat variation can account for significantly different foraging budgets, and Chapman et al. (2002) highlighted that foraging budgets can vary due to biases in sampling and observer differences.

Hoang Minh Duc (2007) noted dietary diversity among the black-shanked doucs at 10.7% in Nui Chua and 7.6% in Phuoc Binh. As discussed in Chapter 6, the habitat at Phuoc Binh is comparable to the habitat on Son Tra and interestingly the range of food plant families in Phuoc Binh is most comparable with the findings on Son Tra. Rawson (2009) suggested a low dietary diversity among the black-shanked doucs in Mondulkiri. Conversely, Ha Thang Long (2009) and Nguyen Thi Tinh et al. (2012) noted a very high dietary diversity. Results of this study suggest the red-shanked doucs on Son Tra are highly selective with a low dietary diversity.

7.4.4. Chemical and nutritional variation

Otto (2005) first reported on the nutritional quality of selected young and selected mature leaves in *Pygathrix*, noting that young leaves were preferred and contained more protein and less NDF than mature leaves. Hoang Minh Duc (2007) reported on selected and non-selected leaves of black-shanked doucs, noting selected leaves contained less protein than non-selected leaves, although it was not significantly different. However, he found that selected leaves contained significantly more cellulose than non-selected leaves. Nguyen Thi Tinh et al. (2012) reported on selected young and selected mature leaves among grey-shanked doucs, noting that selected young leaves were slightly higher in protein but similar in NDF and ADF content to mature leaves, and they were not significantly different for both protein and fiber content. In this study, selected leaves were enriched in protein but low in NDF and ADF compared to non-selected leaves, suggesting tendencies for higher quality leaf selection, although these differences were not significant. Selection for young leaves may be driven by additional variables not tested.

In this study, tannin content did not influence food choices. The most selected leaf species had the highest tannin values, and selected leaves in general also had higher tannin content than non-selected leaves, although these differences were not significant. This is similar to results reported by Hoang Minh Duc (2007), for which the most selected leaf species contained the highest tannin content. The influence of tannins on colobine food selection has been shown to be minimal (Fashing, 2011; Fashing et al., 2007a; Kirkpatrick, 2011), in part relating to digestive adaptations reducing the negative effects of tannins (Chapter 2).

7.4.5. Influences of protein and fiber, habitats, and hunting

Protein and fiber requirements for *Pygathrix* are unknown (Chapter 2). As illustrated by Davies (1994), Lambert (1998), and Milton (1984a) fiber is important in the diets of colobines to maintain gastrointestinal health. The National Research Council (NRC, 2003) suggested that colobines need 15 to 22% crude protein of dry matter, although several studies have shown this number to be too high (Hoang Minh Duc, 2007; Nguyen Thi Tinh et al., 2012; Workman, 2010a; this study). NRC (2003) also reported that colobine foods consists of about 44% NDF and 34%

ADF, although these values have been shown to be too low (Hoang Minh Duc, 2007; Nguyen Thi Tinh et al., 2012; Workman, 2010a; this study). Milton (1979) calculated the protein requirements for howler monkeys (one of the most folivorous New World monkeys) between 9 and 11 % of dry matter. This is comparable to the crude protein levels reported among selected leaves in this study. Milton (1979) also reported that between 4 and 8 % protein per dry weight is needed to maintain positive nitrogen balance. Oftedal et al. (1991) reported primates need to maintain a 7 to 11 % protein/dry matter intake for optimal growth and maintenance, and as much as 14% during reproduction. As noted in Chapter 2, numerous studies have shown that colobines are capable of synthesizing protein through microbial activity. *Pygathrix* therefore might require less protein per weight dry matter. Protein levels in selected young and mature leaves are sufficiently high on Son Tra to meet daily protein requirements, and possibly the additional nutritional requirements of reproduction and lactation.

Numerous authors have illustrated the influence of protein and fiber on food choice and biomass (Brugiere et al., 2002; Chapman et al., 2002; Fashing, 2007; Fashing and Cords, 2000; Milton, 1978; Oates et al., 1990; Waterman et al., 1988; Waterman & Kool, 1994). The protein-to-fiber ratios of selected leaves in this study were not significantly different from non-selected leaves. Also protein-to-fiber ratio of selected young leaves did not differ from the ratio of selected mature leaves. Similar results were found by Workman (2010a) for Delacour’s langurs. If samples tested for quality in my study are representative of overall leaf quality on Son Tra, then mature leaves are of high quality and this reduces the effects that protein and fiber have on leaf choice compared to other sites. The climate on Son Tra remains fairly mild and humid throughout the year, which would also support consistent plant development and higher quality mature foliage due to optimal growing conditions.

Habitat disturbances must also be considered a primary factor affecting diet, and habitat disturbance and hunting have been found to have greater effects on primate biomass than protein-to-fiber ratios (Anderson et al., 2007; Gogarten et al., 2012; Michalski & Peres, 2005), and have an effect on food choice and food availabilities themselves (Riley, 2007; Tutin, 1999; Wong et al., 2006). Fragmentation, habitat loss, and hunting are anthropogenic factors greatly affecting all remaining wild populations of *Pygathrix*. Disturbance in the form of habitat fragmentation is a factor which threatens Son Tra's ecosystem, and influences the behaviors of the red-shanked doucs. To which degree it affects activity and feeding budgets remains to be studied.

7.5. Conclusion

Red-shanked doucs on Son Tra are highly folivorous. Leaves are the most commonly selected food resource (87.8%), followed by fruits and seeds (10.2%), flowers (1.6%) and bark/pith (0.4%). Young leaves are selected over mature leaves (68.6%), and whole leaf blades (86.5%) and petioles (13.1%) were more commonly selected parts of a leaf. There were no significant annual differences in selection of foods or food parts, and only a few significant seasonal differences. The adult females selected young leaves significantly more than adult males in the dry season, possibly relating to the selection of bark by adult males during the dry season, the relationship of bark selection and displaying, and the increase of displaying among adult males during this time. All individuals also selected petioles significantly more in the wet season, although this cannot be considered a fall-back food because fruit availability is highest during this time. Relating to the influence of petiole selection in the wet season, whole leaf blades were selected significantly more in the dry season. Mature leaves are likely a fall-back resource.

Important food plant species on Son Tra include *Parashorea stellata*, *Parsonsia laevigata*, *Ipomoea eberhardtii*, *Garcinia morella*, *Ficus variegata*, *Ficus depressa*, and *Ancistrocladus tectorius*. The six most important plant families are Dipterocarpaceae, Apocynaceae, Convolvulaceae, Guttiferae, Moraceae and Ancistrocladaceae. Moraceae is also an important fruiting food family for the doucs. Chemical and nutritional values of selected and non-selected leaves, and selected young and mature leaves, were not significantly different indicating that mature leaves on Son Tra are of high quality.

The fact that mature leaves are of high quality and young leaves are available throughout the year on Son Tra may contribute to the high degree of folivory and the lack of seasonal variation in leaf selection. Fruits and seeds are also important in the diet and this is highlighted by the lack of correlation between selection and availability.

The doucs are highly selective feeders, and the loss of important food resources on Son Tra would have devastating consequences for the population.

8. Conclusion

8.1. Summary

Son Tra Nature Reserve provides a rare opportunity to study the endangered red-shanked doucs in their natural setting. Results of this study add considerably to the growing knowledge of the biology and behavior of this genus. Many ecological patterns of the red-shanked doucs are comparable to those of other colobines.

According to my study, doucs live in a modular society with groups composed of multiple family units. Family units were both one-male units and multi-male units with an adult male to adult female sex ratio of 1:1.63 individuals, and a young individual to adult ratio of 1:1.26 individuals. Groups are always multi-male/multi-female. The average unit size is 6.5 individuals, and the average group size is 18 individuals and consists of 2.7 units. Social structures and organization may be influenced by male and/or female contest competition and intensified by living in modular societies, by ecological constraints including habitat quality, availability, and disturbance as well as the risk of predation, scramble competition, phylogenetic inertia, or a combination of these factors.

Units of groups fissure and fuse daily. This pattern involves fusion overnight, increased fission in the morning, increased fusion during mid-day, increased fission during the early afternoon, with fusion again in the late afternoon. Units were always fused in the evening. There is a greater degree of fission-fusion behaviors between October and December, suggesting unit cohesion is lowest at that time. Unit cohesion increases significantly during peaks in leaf flush, which is most of the year, and decreases significantly during increased precipitation. Daily fission-fusion involves and strengthens male and/or female bond formations, possibly related to intergroup resource defense, particularly food, territory, and/or mate resources.

The home range of the primary research group is 36 ha with a core area of 8 ha. Monthly variations in the use of their home range were not correlated to phenology or weather variables. Home range overlap between the primary research group and adjacent groups appears to be minimal, or at least adjacent groups were only near the primary group when they were both near the border of the home range. The average daily path length is 509 m, with the average daily path length being longer in the dry season than the wet season. On a daily scale, path length is significantly and negatively correlated to precipitation.

Interspecific associations with rhesus macaques and common muntjacs were infrequent but had a distinct peak between August and October. Both associations are likely the result of chance encounters, although they may offer protection benefits for the primates, and for the muntjacs they provide foraging benefits.

Data in this study were not sufficient to analyze trends and influences of super trooping, all-male group formation, bachelor males, shadowing behaviors, dispersal and immigration of individuals, and mating or birthing peaks. However, the limited data suggests there is a risk of take-overs relating to shadowing all-male groups and bachelor males, that dispersal may be seasonal, and that there may be peaks in birthing.

Concerning the activity budget in all individuals, inactivity was the most common behavior (35.3%), followed by moving (28.6%), socializing (21.7%), feeding (13.7%) and self-grooming (0.7%). There were many significant differences in activity budgets between seasons and groups of individuals. Considering the annual scale, adults vocalized significantly more than young individuals, and young individuals played significantly more than adults. Adult males were significantly more vigilant than adult females, and adult females allogroomed significantly more than adult males. On a monthly scale, in all individuals moving positively correlated to temperature and negatively correlated to flowering, traveling positively correlated to variation in the use of home range, displaying positively correlated to leaf flush, and vocalizing negatively correlated to leaf flush. Adults followed these patterns with the addition of self-grooming being positively correlated to temperature. In young individuals, vocalizing negatively correlated to temperature, playing positively correlated to temperature, and allogrooming positively correlated to flowering. In adult males, self-grooming positively correlated to temperature, moving negatively correlated to flowering, traveling positively correlated to variations in the use of home range, displaying positively correlated to leaf flush, and vocalizing negatively correlated to leaf flush. In adult females, self-grooming positively correlated to precipitation, moving positively correlated to temperature and to variation in the use of home range, and moving negatively correlated to flowering. On the daily scale doucs show a typical *Pygathrix* pattern regarding the timing of feeding and resting peaks.

They also exhibit a daily fission-fusion pattern which significantly correlates with their daily activity budgets. When units are fused they rest significantly more, and when fissioned they move, feed, vocalize, and are vigilant significantly more. This pattern appears to be an adaptation to avoid scramble competition and to maintain contact and coordination between units.

The percentage of feeding as part of the activity budget is reduced compared to most colobines, but similar to the percentage of feeding reported in grey-shanked doucs. The reduced percentage of feeding as part of the activity budget is likely related to the quality of habitat on Son Tra, and the relatively high nutritional quality of mature leaves. The doucs were more social than most colobines but again similar to grey-shanked doucs. Living in a modular society partly explains the increased social budget. Also, a mild climate and reduced thermoregulatory stress might permit reduced resting and increased social activity. The increase in vigilance and vocalizations might be related to predation risks, intergroup resource defense, and intragroup unit coordination. The high degree of vocalizations highlights there importance in modular societies for the doucs on Son Tra. The moving budget was slightly higher than other colobines, but similar to the grey-shanked and other red-shanked douc studies. The distribution of food resources on Son Tra, and the influences of scramble competition and intergroup resource defense, likely influence the frequency of moving.

The red-shanked doucs activity budget is most comparable to the grey-shanked doucs in Kon Ka Kinh, including a high degree of sociality, reduced inactivity especially resting, and reduced feeding compared to other colobines. Reasons for this similarity are likely related to similar habitat and climatic characteristics in these study sites including precipitation, temperature, forest quality, density, species composition and characteristics.

Concerning feeding ecology, leaves were the most common resource (87.8%), followed by fruits and seeds (10.2%), flowers (1.6%) and bark/pith (0.4%). This feeding budget is generally similar to other colobines, although the red-shanked doucs are highly folivorous. Young leaves were selected over mature leaves (68.6%), and whole leaf blades (86.5%) and petioles (13.1%) were more commonly selected leaf parts. Adult females selected young leaves significantly more than adult males in the dry season, likely as a result of male selection of bark and increase in display behavior during this time. No other differences were found between adult males and females, or adults and young individuals. All individuals selected petioles significantly more in the wet season, and as a result whole leaf blades were selected significantly more in the dry season. Petioles are selected largely in November during a peak in fruiting, and mature leaves likely represent a fall-back resource. Seasonally, the selection of flowers and bark/pith increased in the dry season along with flowering peaks. Young leaf selection, and fruit and seed selection, is not correlated to availability. This suggests that the doucs are selective feeders.

Important food species on Son Tra include *Parashorea stellata*, *Parsonsia laevigata*, *Ipomoea eberhardtii*, *Garcinia morella*, *Ficus variegata, Ficus depressa*, and *Ancistrocladus tectorius*. The six most important families are Dipterocarpaceae, Apocynaceae, Convolvulaceae, Guttiferae, Moraceae and Ancistrocladaceae. Dietary diversity is low and the selection of feeding trees is not related to tree densities aside from dipterocarp, again suggesting the doucs seek dispersed resources and are selective foragers.

Chemical and nutritional contents of selected and non-selected leaves, and selected young and mature leaves, were not significantly different. The high degree of folivory and the lack of seasonal variation in leaf selection might be related to the high quality of mature leaves. Anthropogenic effects, and the type of habitat, might also influence the degree of folivory given that fruit availability on Son Tra is lower than at other *Pygathrix* research sites (see Chapter 4). The importance of fruits and seeds is highlighted by the lack of correlation between selection and availability.

8.2. Hypotheses revisited

Concerning social structures and organization, the hypotheses that formed the base of the research were that groups were multi-male/multi-female due to patterns of fission-fusion and the occurrence of multi-male units, which is supported. I hypothesized there would be a daily pattern of fission-fusion, and therefore the degree of fission-fusion would not be related to phenology or weather variables. This is partly supported and partly rejected because there is daily fission-fusion, but the degree of fission-fusion is significantly and positively correlated to precipitation and significantly and negatively correlated to leaf flush. It was further predicted that units/groups would have a 1:2 adult male to adult female ratio, and this is supported. Finally, I hypothesized daily path lengths and variation in the use of home range would correlate to phenology and weather. This is rejected aside from a significant negative correlation between daily path lengths and precipitation.

Concerning hypotheses relating to activity budget, I predicted resting and feeding would be common activities, with moving and socializing being less common. This is rejected as social activity and moving were more common than feeding. I also assumed play activities would be more common among young individuals, which is supported. I hypothesized that the activity budgets in adult males and adult females would not significantly differ, and this is largely supported. Finally, I predicted activity budgets would be seasonal. Although this hypothesis lacked clarity, it is generally rejected.

Concerning the hypotheses relating to feeding ecology, I predicted doucs were selective foragers and that a few keystone resources would account for a majority of their diet. This is supported as most leaf, flower, fruit and seed feeding were from seven species of six families including *Parashorea stellata*, *Parsonsia laevigata*, *Ipomoea eberhardtii*, *Garcinia morella*, *Ficus variegata*, *Ficus depressa* and *Ancistrocladus tectorius*. I hypothesized that food selection would be correlated to phenology, and this is rejected with the exception of flower selection occurring during flowering peaks. It was further assumed that food selection would be influenced by protein and fiber content, which is rejected because the protein-to-fiber ratio of selected and non-selected leaves did not differ significantly. I also suggested young leaves would be selected over mature leaves because they would contain more protein and less fiber than mature leaves. Although young leaves were selected more commonly than mature leaves, young leaves and mature leaves did not significantly differ in protein-to-fiber ratios. It was further predicted that secondary compounds would not influence selection, and this is supported as tannin content was not significantly different between selected and non-selected foods. Finally, I hypothesized that mature leaves would form fall-back foods during resource scarcity, and this is partially supported and partially rejected. Mature leaves are likely fall-back resources, but mature leaves are also of high nutritional quality.

8.3. Looking to the future

Habitat loss and fragmentation on Son Tra have severe impacts to the doucs, and these impacts are likely to worsen unless they are addressed. Loss of a single important food species on Son Tra, such as the critically endangered *P. stellata*, will likely have devastating effects on the douc population because they rely on a small number of keystone food species. It has been shown that the population of doucs on Son Tra is likely one of the most prosperous in their Vietnamese distribution range due to military protection, and favorable climate and habitat. This site and the population play a critical role in the survival of the species.

One of the outputs of this research is to provide materials to the Department of Science and Technology (DOST), the Department of Agriculture and Rural Development (DARD), the Forest Protection Department (FPD), Son Tra Ecotourism Management Board (STEMB), and the People’s Committee of Da Nang. Since 2010, information gathered in this study has been used to develop conservation activities which are implemented in cooperation with various city departments. Photo exhibitions were created in Da Nang for the local population and for elementary and middle school students in association with DOST and their conservation consultant, Ulrike Streicher. These were designed to raise awareness about the existence and plight of the red-shanked doucs on Son Tra, and the biodiversity on Son Tra. Son Tra is known as Monkey Mountain (núi Khỉ) in Vietnamese, but at the start of this study several government officials doubted the existence of the doucs on Son Tra. Since the start of this study, the doucs are being transformed into a flagship species for Da Nang, and awareness has increased exponentially. DOST, DARD, STEMB and Ulrike Streicher have recently built the first canopy bridges in Vietnam on Son Tra, based on recommendations resulting from this study. These bridges aid the red-shanked doucs in safely crossing the roads in areas where the road construction has been most damaging (Dac Manh, 2012; Thanh Hai, 2013; Mai Trang, 2013). In the last weeks of August 2013, more monkey bridges have been approved and the first phase of a roadside habitat restoration program has also been approved. Finally, DARD, FPD, STEMB and Ulrike Streicher are beginning to implement jointly managed road controls on Son Tra to address illegal activities and further enhance the protection of biodiversity. Training provided to these new patrol guards incorporates findings from this study.

Whereas the red-shanked doucs face the risk of extinction throughout their distribution range, the local government in Da Nang is taking steps to ensure the long-term survival of biodiversity on Son Tra with the red-shanked doucs as a flagship species. Results from this study have aided and will continue to aid conservation efforts by improving the understanding of red-shanked douc socioecology and their needs. Hope for the red-shanked douc rises on Monkey Mountain in the land of the ascending dragon.

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Appendices

Appendices include a separate list for insects, freshwater fish and crustaceans, amphibians, reptiles, birds, mammals, and plants. Insects are divided by order, but in a few instances the suborder is used in addition to the order, or if the order is unknown the subphylum or phylum is used. Amphibians are divided by family because all are currently from the Anura order. Reptiles are divided by both order and either suborder or family. Birds are divided by order and family, and mammals are divided by order. Some mammal species are no longer likely to be on Son Tra (e.g. gibbons). Plants are divided according to Anthophyta phyla (flowering plants including the Dicotyledones and Monocotyledones classes separately), Coniferophyta phyla (gymnosperms), and Pterophyta phyla (ferns).

Many species of insects, freshwater fish and decapods, amphibians, reptiles, birds and plants were first observed or identified during this study. For insects, there are orders and phyla with unusually few representatives for an evergreen to semi-evergreen tropical rainforest (e.g. spiders, ants), for amphibians there are no records from the Caudata and Gymnophiona orders, and for plants there are no records of Bryophyta (mosses) and Hepaticophyta (liverworts) phyla. These new identifications and the absence of other identifications illustrate that this list is incomplete and the full range of biodiversity is unknown and not yet represented.

Sources are as follows: 1=Van Peenen et al. (1971), 2=Dinh Thi Phuong Anh (1997), 3=Vu Ngoc Thanh et al. (2007), 4=specimens identified during this study and during Dr. Ulrike Streicher’s ongoing conservation project with Da Nang City Department of Science and Technology, Department of Agriculture and Rural Development, and Son Tra Ecotourism Management Board, 5=Traffic (2004), 6=Lippold (1977), and 7=ENV (2006).

Appendix 1. Insects

Order and Common name	Species	IUCN listing	Source
Annelida (phylum)			
[Ringed worm sp.]	Clitellata class		4
[Leech sp.]	Clitellata class		4
Araneae			
[Spider sp.]	Araneidae spp.		4
[Spider sp.]	Pholcidae spp.		4
[Spider sp.]	Salticidae spp.		4
[Spider sp.]	Thomisidae spp.		4
Blattodea -Blattaria			
[Cockroach sp.]	*Hemithyrsocera* sp.		2
[Cockroach sp.]	*Phyllodromica* sp.		2
Blattodea - Isoptera			
[Termite sp.]	*Odontotermes* sp.		2
[Termite sp.]	*Termes* sp.		2
Coleoptera			
[Scarab beetle sp.]	*Adoretus tenuimaculatus*		2
[Scarab beetle sp.]	*Adoretus* sp.		2
[Scarab beetle sp.]	*Agestrata* sp.		2
[Rhinoceros beetle sp.]	*Allomyrina* sp.		2
[Scarab beetle sp.]	*Alissonotum* sp.		2
White muscardine fungus beetle	*Anomala antigua*		2
Golden flower beetle	*Anomala cupripes*		2
[Long-horn beetle sp.]	*Aristobia* sp.		2
[Tiger beetle sp.]	*Cicindela* sp.		2
Bean blister beetle	*Epicauta gorhami*		2
[Blister beetle sp.]	*Epicauta imphessicornis*		2
[Ladybird beetle sp.]	*Epilachna* sp.		2
[Ladybird beetle sp.]	*Henosepilachna pusillanima*		2
[Scarab beetle sp.]	*Holotricha* sp.		2
Gold dust weevil beetle	*Hypomeces squamosus*		2
[Blister beetle sp.]	*Mylabris cichorii*		2
Chinese blister beetle	*Mylabris phalerata*		2
[Long-horn beetle sp.]	*Nadezhdiella cantori*		2
Asiatic rhinoceros beetle	*Oryctes rhinoceros*		2
Siamese rhinoceros beetle	*Xylotrupes gideon*		2
Diptera			
Common housefly	*Musca domestica*		2
Hemiptera			
[Leaf-footed bug sp.]	*Acanthocoris* sp.		2
[Leaf-footed bug sp.]	*Acestra* sp.		2
[Leaf-footed bug sp.]	*Anoplocnemis* sp.		2
[Shield bug sp.]	*Aspongopus nigriventris*		2
[Vegetable bug sp.]	*Cappaca taprobanensis*		2
[Leaf-footed bug sp.]	*Cletus punctulatus*		2

[Leaf-footed bug sp.]	*Cletus graminis*		2
[Cicada sp.]	*Cryptotympana holsti*		2
[Cicada sp.]	*Cryptotympana mandarina*		2
Red cotton stainer	*Dysdercus cingulatus*		2
[Cotton stainer sp.]	*Dysdercus* sp.		2
[Cotton stainer sp.]	*Dysdercus* sp.		2
Yellow marmorated shield bug	*Erthesina fullo*		2
[Leaf-footed bug sp.]	*Homoeocerus (Anacanthocoris) humeralis*		2
[Leaf-footed bug sp.]	*Homoeocerus (Anacanthocoris) striicornis*		2
Paddy bug	*Leptocorisa acuta*		2
Rice Gandhi bug	*Leptocorisa varicornis*		2
Green vegetable bug	*Nezara viridula*		2
[Vegetable bug sp.]	*Nezara viridula torquata*		2
[Shield bug sp.]	*Niphe* sp.		2
[Shield bug sp.]	*Palomena* sp.		2
Brown-winged green bug	*Plautia crossota*		2
Citrus green bug	*Rhynchocoris humeralis*		2
Yellow-belly arctiid	*Solenosthedium chinensis*		2
Lychee stink bug	*Tessaratoma papillosa*		2
[True bug sp.]	*Tessaratoma quadrata*		2
[True bug sp.]	*Tetroda* sp.		2
[True bug sp.]	*Tolumnia* sp.		2
Hymenoptera			
Asiatic honey bee	*Apis cerana*		2
[Bumble bee sp.]	*Bombus* sp.		2
Asian predatory wasp	*Vespa velutina*		2
[Hornet sp.]	*Vespa* sp.		2
[Carpenter bee sp.]	*Xylocopa orichalcea*		2
[Ant spp.]	Unidentified ant spp.		4
Lepidoptera			
Plain puffin butterfly	*Appias indra*		4
Common albatross	*Appias paulina*		4
Common rose butterfly	*Atrophaneura aristolochiae*		2
Common batwing butterfly	*Atrophaneura varuna*		2
Lemon emigrant butterfly	*Catopsilia pomona*		4
Common map butterfly	*Cyrestis thyodamas*		4
Orange lacewing butterfly	*Cethosia penthesilea*		4
Common tiger buttefly	*Danaus genutia*		4
Monarch butterfly	*Danaus plexippus*	Near Threatened ver 3.1	2
Redbase jezebel butterfly	*Delias aglaia*		2
[unnamed butterfly]	*Eucyclodes albisparsa*		4
Brown king crow butterfly	*Euploea klugii erichsonii*		2
Blue banded king crow	*Euploea eunice*		4
Blue spotted crow	*Euploea midamus*		2
Striped blue crow butterfly	*Euploea mulciber*		2
Magpie crow butterfly	*Euploea radamanthus*		4

Common grass yellow	*Eurema hecabe*		4
White-edged blue baron	*Euthalia phemius*		4
Common faun butterfly	*Faunis canens arcesilas*		4
Tailed jay butterfly	*Graphium agamemnon*		4
Five-bar swordtail	*Graphium (Pathysa) antiphates*		2
Great orange tip butterfly	*Hebomoia glaucippe*		4
Diadem butterfly	*Hypolimnas misippus*		2
Blue glassy tiger butterfly	*Ideopsis similis persimilis*		2
Yellow orange tip butterfly	*Ixias pyrene*		2
White dragontail butterfly	*Lamproptera curius*		2
Tropical swallowtail moth	*Lyssa zampa*		4
Common raven butterfly	*Papilio castor*		2
Common mime butterfly	*Papilio clytia*		2
Lime butterfly	*Papilio demoleus*		2
Red helen butterfly	*Papilio helenus*		2
Great Mormon	*Papilio memnon*		2
Paris peacock butterfly	*Papilio paris*		2
Common mormon	*Papilio polytes*		2
Glassy tiger butterfly	*Parantica aglea*		2
Chocolate tiger butterfly	*Parantica melaneus*		2
Common leopard	*Phalanta phalantha*		4
Indian cabbage white	*Pieris canidia*		2
Small white butterfly	*Pieris rapae*		2
[Sawtooth butterfly sp.]	*Prioneris philonome clemanthe*		2
Borneo birdwing butterfly	*Troides andromache*		2
Cruiser butterfly	*Vindula erota*		4
Punchinello butterfly	*Zemeros flegyas*		4
Mantodea			
Praying mantis	*Mantis religiosa*		2
Chinese mantis	*Tenodera sinensis*		2
Neuroptera			
[Green lacewing sp.]	*Chrysopa* sp.		2
Odonata			
[Damselfly sp.]	*Aciagrion* sp.		2
[Damselfly sp.]	*Agriocnemis* sp.		2
[Dragonfly sp.]	*Brachythemis* sp.		2
	Coeliccia chromothorax		4
Scarlet dwarf dragonfly	*Nannophya pygmaea*	Least Concern ver 3.1	2
	Orthetrum glaucum		4
	Orthetrum sabina		4
	Protosticta grandis		4
	Vestalis gracilis		4
Orthoptera - Caelifera			
[Grasshopper sp.]	*Acrida chinensis*		2
[Grasshopper sp.]	*Aiolopus tamulus*		2
Long-headed grasshopper	*Atractomorpha lata*		2
Vegetable grasshopper	*Atractomorpha sinensis*		2

[Grasshopper sp.]	*Euprepoenemis* sp.		2
[Grasshopper sp.]	*Gastrimargus africanus orientalis*		2
[Grasshopper sp.]	*Oxya diminula*		2
[Grasshopper sp.]	*Oxya velox*		2
[Grasshopper sp.]	*Phlaeoba* sp.		2
[Grasshopper sp.]	*Sphathosternum* sp.		2
[Grasshopper sp.]	*Xenocatantops* sp.		2
Orthoptera - Ensifera			
Tawian giant cricket	*Brachytrupes portentosus*		2
[Katydid sp.]	*Conocephalus (Anisoptera) maculatus*		2
[Katydid sp.]	*Euconocephalus pallidus*		2
[Cricket sp.]	Gryllidae family		2
[Cricket sp.]	*Gryllodes* sp.		2
African mole cricket	*Gryllotalpa africana*		2
[Cricket sp.]	*Gryllus* sp.		2
Japanese broadwinged katydid	*Holochlora japonica*		2
Scolopendromorpha			
Vietnamese Centipede	*Scolopendra subspinipes*		4
Tricladida			
Hammerhead worm	*Bipalium adventitium*		4
Hammerhead slug	*Bipalium kewense*		4

Appendix 2. Amphibians, freshwater fish, and freshwater decapods

Order and Common name	Species	IUCN listing	Source
Amphibians			
Bufonidae			
Asian toad	*Duttaphrynus melanostictus*	Least Concern ver 3.1	2
Dicroglossidae			
Kuhl's creek frog	*Limnonectes kuhlii*	Least Concern ver 3.1	2
[unnamed]	*Limnonectes poilani*	Least Concern ver 3.1	4
Hylidae			
Annam tree frog	*Hyla simplex*	Least Concern ver 3.1	2
Microhylidae			
Asian painted frog	*Kaloula pulchra*	Least Concern ver 3.1	4
Ranidae			
Cricket frog	*Fejervarya limnocharis*	Least Concern ver 3.1	2
[unnamed]	*Hylarana attigua*	Vulnerable ver 3.1	4
Günther's frog	*Hylarana guentheri*	Least Concern ver 3.1	2
Sapgreen stream frog	*Hylarana nigrovittata*	Least Concern ver 3.1	2
Green puddle frog	*Occidozyga lima*	Least Concern ver 3.1	2
East Asian bullfrog	*Rana rugulosa*		2
Rhacophoridae			
Green-limbed tree frog	*Kurixalus bisacculus*	Least Concern ver 3.1	4
Bana leaf frog	*Philautus banaensis*		4
Four-lined tree frog	*Polypedates leucomystax*	Least Concern ver 3.1	2
Fish			
[Unidentified freshwater fish sp.]			4
Decapods			
[Unidentified Grapsoidea sp.]	Grapsoidea sp.		4
[Unidentified freshwater shrimp spp.]			4

Appendix 3. Reptiles

Order and Common name	Species	IUCN listing	Source
Squamata - Lacertilia			
Agamidae			
Scale-bellied tree lizard	*Acanthosaura lepidogaster*	Least Concern ver 3.1	2
Oriental garden lizard	*Calotes versicolor*		2
Spotted gliding lizard	*Draco maculatus*	Least Concern ver 3.1	3
Peters butterfly lizard	*Leiolepis guentherpetersi*		2
Squamata - Sauria			
Scincidae			
Bronze mabuya	*Eutropis macularia*		2
East Indian brown mabuya	*Eutropis multifasciata*		2
Black ground skink	*Scincella melanosticta*		4
Cochinchinese water skink	*Tropidophorus cocincinensis*		2
Squamata - Scleroglossa			
Gekkonidae			
Tockay gecko	*Gekko gecko*		4
Common house gecko	*Hemidactylus frenatus*	Least Concern ver 3.1	2
Varanidae			
Chinese water dragon	*Physignathus cocincinus*		2
Water monitor	*Varanus salvator*	Least Concern ver 3.1	2
Squamata - Serpentes			
Colubridae			
Oriental whipsnake	*Ahaetulla prasina*	Least Concern ver 3.1	2
Many-spotted cat snake	*Boiga multomaculata*		3
New Guinea bockadam	*Cerberus rynchops*	Least Concern ver 3.1	4
Golden tree snake	*Chrysopelea ornata*		4
Painted bronzeback	*Dendrelaphis pictus*		4
Blanford's bridal snake	*Dryocalamus davisonii*	Least Concern ver 3.1	3
Radiated ratsnake	*Elaphe radiata*		2
Common wolf snake	*Lycodon capucinus*		3
Spotted slug snake	*Pareas margaritophorus*	Least Concern ver 3.1	3
Common mock viper	*Psammodynastes pulverulentus*		4
Chinese ratsnake	*Ptyas korros*		2
Oriental ratsnake	*Ptyas mucosus*		2
Red-necked keelback	*Rhabdophis subminiatus*		4
Black-headed collared snake	*Sibynophis melanocephalus*	Least Concern ver 3.1	4
Checkered keelback	*Xenochrophis piscator*		2
Elapidae			
Banded krait	*Bungarus fasciatus*		2
Speckled coral snake	*Calliophis maculiceps*		4
Monocled cobra	*Naja kaouthia*	Least Concern ver 3.1	4
Pythonidae			
Asiatic rock python	*Python molurus*	Near threatened ver 2.3	2
Reticulated python	*Python reticulatus*		2
Viperidae			

Chinese mountain pit viper	*Ovophis monticola*	Least Concern ver 3.1	2
White-lipped pit viper	*Trimeresurus albolabris*	Least Concern ver 3.1	4
Pope's pit viper	*Trimeresurus popeorum*		4
Testudines - Cryptodira			
Cheloniidae			
Green sea turtle	*Chelonia mydas*	Endangered A2bd ver 3.1	2
Olive Ridley sea turtle	*Lepidochelys olivacea*	Vulnerable A2bd ver 3.1	5
Geoemydidae			
Annam leaf turtle	*Mauremys annamensis*	Critically Endangered A1d+2d ver 2.3	2
Keeled box turtle	*Pyxidea mouhotii*		4
Testudinidae			
Impressed tortoise	*Manouria impressa*	Vulnerable A1acd B1+2acd ver 2.3	2
Trionychidae			
Wattle-necked softshell turtle	*Palea steindachneri*	Vulnerable A1cd+2cd ver 2.3	2

Appendix 4. Birds

Family and Common name	Species	IUCN listing	Source
Accipitriformes / Falconiformes			
Accipitridae			
Shikra	*Accipiter badius*	Least Concern ver 3.1	2
Crested goshawk	*Accipiter trivirgatus*	Least Concern ver 3.1	4
Jerdon’s baza	*Aviceda jerdoni*	Least Concern ver 3.1	4
Black eagle	*Ictinaetus malayensis*	Least Concern ver 3.1	4
Black kite	*Milvus migrans*	Least Concern ver 3.1	2
Mountain hawk-eagle	*Nisaetus nipalense*	Least Concern ver 3.1	4
Falconidae			
Peregrine falcon	*Falco peregrinus*	Least Concern ver 3.1	4
Oriental hobby	*Falco severus*	Least Concern ver 3.1	2
Apodiformes			
Apodidae			
Little swift	*Apus affinis*	Least Concern ver 3.1	2
Caprimulgiformes			
Caprimulgidae			
Savanna nightjar	*Caprimulgus affinis*	Least Concern ver 3.1	2
Charadriiformes			
Charadriidae			
Kentish plover	*Charadrius alexandrinus*	Least Concern ver 3.1	4
Little ringed plover	*Charadrius dubius*	Least Concern ver 3.1	2
Greater sand plover	*Charadrius leschenaultii*	Least Concern ver 3.1	2
Lesser sand plover	*Charadrius mongolus*	Least Concern ver 3.1	2
Red-wattled lapwing	*Vanellus indicus*	Least Concern ver 3.1	4
Scolopacidae			
Common sandpiper	*Actitis hypoleucos*	Least Concern ver 3.1	2
Pin-tailed snipe	*Gallinago stenura*	Least Concern ver 3.1	2
Red-necked phalarope	*Phalaropus lobatus*	Least Concern ver 3.1	4
Sternidae			
Little tern	*Sterna albifrons*	Least Concern ver 3.1	2
Columbiformes			
Columbidae			
Common emerald dove	*Chalcophaps indica*	Least Concern ver 3.1	2
Spotted dove	*Stigmatopelia chinensis*	Least Concern ver 3.1	2
Red turtle dove	*Streptopelia tranquebarica*	Least Concern ver 3.1	2
Thick-billed green pigeon	*Treron curvirostra*	Least Concern ver 3.1	2
Pink-necked green pigeon	*Treron vernans*	Least Concern ver 3.1	2
Coraciiformes			
Alcedinidae			
Common kingfisher	*Alcedo atthis*	Least Concern ver 3.1	2
Halcyonidae			
White-throated kingfisher	*Halcyon smyrnensis*	Least Concern ver 3.1	2
Meropidae			
Blue-tailed bee-eater	*Merops philippinus*	Least Concern ver 3.1	2
Blue-throated bee-eater	*Merops viridis*	Least Concern ver 3.1	2

Blue-bearded bee-eater	*Nyctyornis athertoni*	Least Concern ver 3.1	2
Upupidae			
Eurasian hoopoe	*Upupa epops*	Least Concern ver 3.1	2
Cuculiformes			
Cuculidae			
Plaintive cuckoo	*Cacomantis merulinus*	Least Concern ver 3.1	4
Lesser coucal	*Centropus bengalensis*	Least Concern ver 3.1	2
Greater coucal	*Centropus sinensis*	Least Concern ver 3.1	2
Large hawk-cuckoo	*Cuculus sparverioides*	Least Concern ver 3.1	2
Green-billed malkoha	*Phaenicophaeus tristis*	Least Concern ver 3.1	2
Galliformes			
Phasianidae			
Green-legged hill partridge	*Arborophila chloropus*	Least Concern ver 3.1	2
King quail	*Coturnix chinensis*	Least Concern ver 3.1	2
Red junglefowl	*Gallus gallus*	Least Concern ver 3.1	2
Germain's peacock-pheasant	*Polyplectron germaini*	Near Threatened ver 3.1	2
Gruiformes			
Rallidae			
Slaty-breasted rail	*Gallirallus striatus*	Least Concern ver 3.1	2
Baillon's crake	*Porzana pusilla*	Least Concern ver 3.1	2
Passeriformes			
Aegithinidae			
Great iora	*Aegithina lafresnayei*	Least Concern ver 3.1	2
Alaudidae			
Oriental skylark	*Alauda gulgula*	Least Concern ver 3.1	2
Chloropseidae			
Blue-winged leafbird	*Chloropsis cochinchinensis*	Least Concern ver 3.1	2
Cisticolidae			
Dark-necked tailorbird	*Orthotomus atrogularis*	Least Concern ver 3.1	4
Hill prinia	*Prinia atrogularis*	Least Concern ver 3.1	2
Yellow-bellied prinia	*Prinia flaviventris*	Least Concern ver 3.1	2
Corvidae			
Common green magpie	*Cissa chinensis*	Least Concern ver 3.1	2
Racket-tailed treepie	*Crypsirina temia*	Least Concern ver 3.1	2
Dicaeidae			
Yellow-vented flowerpecker	*Dicaeum chrysorrheum*	Least Concern ver 3.1	2
Nilgiri flowerpecker	*Dicaeum concolor*	Least Concern ver 3.1	2
Dicruridae			
Crow-billed drongo	*Dicrurus annectans*	Least Concern ver 3.1	2
Black drongo	*Dicrurus macrocercus*	Least Concern ver 3.1	2
Greater racket-tailed drongo	*Dicrurus paradiseus*	Least Concern ver 3.1	2
Lesser racket-tailed drongo	*Dicrurus remifer*	Least Concern ver 3.1	4
Estrildidae			
Tricoloured munia	*Lonchura malacca*	Least Concern ver 3.1	2
Scaly-breasted munia	*Lonchura punctulata*	Least Concern ver 3.1	2
White-rumped munia	*Lonchura striata*	Least Concern ver 3.1	2
Hirundinidae			
Red-rumped swallow	*Cecropis daurica*	Least Concern ver 3.1	2

Common house-martin	*Delichon urbicum*	Least Concern ver 3.1	2
Irenidae			
Asian fairy-bluebird	*Irena puella*	Least Concern ver 3.1	2
Laniidae			
Brown shrike	*Lanius cristatus*	Least Concern ver 3.1	4
Leiothrichidae			
Black-throated laughingthrush	*Garrulax chinensis*	Least Concern ver 3.1	2
White-crested laughingthrush	*Garrulax leucolophus*	Least Concern ver 3.1	2
Monarchidae			
Black-naped monarch	*Hypothymis azurea*	Least Concern ver 3.1	2
Motacillidae			
Red-throated pipit	*Anthus cervinus*	Least Concern ver 3.1	2
Olive-backed pipit	*Anthus hodgsoni*	Least Concern ver 3.1	2
Richard's pipit	*Anthus richardi*	Least Concern ver 3.1	2
Paddyfield pipit	*Anthus rufulus*	Least Concern ver 3.1	2
White wagtail	*Motacilla alba*	Least Concern ver 3.1	2
Western yellow wagtail	*Motacilla flava*	Least Concern ver 3.1	2
Muscicapidae			
White-rumped shama	*Copsychus malabaricus*	Least Concern ver 3.1	2
Oriental magpie-robin	*Copsychus saularis*	Least Concern ver 3.1	2
Blue-and-white flycatcher	*Cyanoptila cyanomelana*	Least Concern ver 3.1	2
Mangrove blue flycatcher	*Cyornis rufigastra*	Least Concern ver 3.1	2
Slaty-backed forktail	*Enicurus schistaceus*	Least Concern ver 3.1	2
Verditer flycatcher	*Eumyias thalassina*	Least Concern ver 3.1	2
Narcissus flycatcher	*Ficedula narcissina*	Least Concern ver 3.1	4
Blue rock thrush	*Monticola solitarius*	Least Concern ver 3.1	2
Asian Stonechat	*Saxicola maurus*	[not evaluated]	4
African stonechat	*Saxicola torquatus*	Least Concern ver 3.1	2
Nectariniidae			
Black-throated sunbird	*Aethopyga saturata*	Least Concern ver 3.1	4
Crimson sunbird	*Aethopyga siparaja*	Least Concern ver 3.1	4
Ruby-cheeked sunbird	*Anthreptes singalensis*	Least Concern ver 3.1	2
Olive-backed sunbird	*Nectarinia jugularis*	Least Concern ver 3.1	2
Oriolidae			
Black-hooded oriole	*Oriolus xanthornus*	Least Concern ver 3.1	2
Pachycephalidae			
Mangrove whistler	*Pachycephala grisola*	Least Concern ver 3.1	2
Passeridae			
Eurasian tree sparrow	*Passer montanus*	Least Concern ver 3.1	2
Pellorneidae			
Rufous-throated fulvetta	*Alcippe rufogularis*	Least Concern ver 3.1	2
Scaly-crowned babbler	*Malacopteron cinereum*	Least Concern ver 3.1	2
Puff-throated babbler	*Pellorneum ruficeps*	Least Concern ver 3.1	4
Buff-breasted babbler	*Pellorneum tickelli*	Least Concern ver 3.1	2
Phylloscopidae			
Arctic warbler	*Phylloscopus borealis*	Least Concern ver 3.1	2
Dusky warbler	*Phylloscopus fuscatus*	Least Concern ver 3.1	2
Pallas’s leaf warbler	*Phylloscopus proregulus*	Least Concern ver 3.1	2

Pycnonotidae			
Grey-eyed bulbul	*Iole propinqua*	Least Concern ver 3.1	2
Mountain bulbul	*Ixos mcclellandii*	Least Concern ver 3.1	4
Sooty-headed bulbul	*Pycnonotus aurigaster*	Least Concern ver 3.1	2
Streak-eared bulbul	*Pycnonotus blanfordi*	Least Concern ver 3.1	2
Stripe-throated bulbul	*Pycnonotus finlaysoni*	Least Concern ver 3.1	2
Red-whiskered bulbul	*Pycnonotus jocosus*	Least Concern ver 3.1	2
Rhipiduridae			
White-throated fantail	*Rhipidura albicollis*	Least Concern ver 3.1	2
Sturnidae			
Jungle myna	*Acridotheres fuscus*	Least Concern ver 3.1	2
Common myna	*Acridotheres tristis*	Least Concern ver 3.1	2
Hill myna	*Gracula religiosa*	Least Concern ver 3.1	2
Chestnut-tailed starling	*Sturnus malabaricus*	Least Concern ver 3.1	2
Black-collared starling	*Sturnus nigricollis*	Least Concern ver 3.1	2
Timaliidae			
Grey-cheeked tit-babbler	*Macronous flavicollis*	Least Concern ver 3.1	2
Pin-striped tit-babbler	*Macronous gularis*	Least Concern ver 3.1	2
Large scimitar babbler	*Pomatorhinus hypoleucos*	Least Concern ver 3.1	2
Turdidae			
Japanese thrush	*Turdus cardis*	Least Concern ver 3.1	2
Common blackbird	*Turdus merula*	Least Concern ver 3.1	4
Orange- headed thrush	*Zoothera citrina*	Least Concern ver 3.1	4
Zosteropidae			
Oriental white-eye	*Zosterops palpebrosus*	Least Concern ver 3.1	2
Pelecaniformes			
Ardeidae			
Chinese pond-heron	*Ardeola bacchus*	Least Concern ver 3.1	2
Striated heron	*Butorides striata*	Least Concern ver 3.1	2
Little egret	*Egretta garzetta*	Least Concern ver 3.1	2
Cinnamon bittern	*Ixobrychus cinnamomeus*	Least Concern ver 3.1	2
Intermediate egret	*Mesophoyx intermedia*	Least Concern ver 3.1	2
Piciformes			
Megalaimidae			
Green-eared barbet	*Megalaima faiostricta*	Least Concern ver 3.1	2
Lineated barbet	*Megalaima lineata*	Least Concern ver 3.1	2
Picidae			
Rufous woodpecker	*Celeus brachyurus*	Least Concern ver 3.1	2
Greater flameback	*Chrysocolaptes lucidus*	Least Concern ver 3.1	2
Psittaciformes			
Psittaculidae			
Red-breasted parakeet	*Psittacula alexandri*	Least Concern ver 3.1	2
Strigiformes			
Strigidae			
Indian/Collared scops-owl	*Otus (bakkamoena) lettia*	Least Concern ver 3.1	2
Barn owl	*Tyto alba*	Least Concern ver 3.1	4
Turniciformes			
Turnicidae			

Barred buttonquail	*Turnix suscitator*	Least Concern ver 3.1	2

Appendix 5. Mammals

Order and Common name	Species	IUCN listing	Source
Artiodactyla			
Indian muntjac	*Muntiacus muntjak*	Least Concern ver 3.1	1
Wild pig	*Sus scrofa*	Least Concern ver 3.1	2
[Mouse deer sp.]	*Tragulus* sp.		3
Carnivora			
Small Asian mongoose	*Herpestes javanicus*	Least Concern ver 3.1	1
[Otter sp.]	Lutra sp.		2
Burmese ferret badger	*Melogale personata*	Data Deficient ver 3.1	1
Masked palm civet	*Paguma larvata*		3
Asian palm civet	*Paradoxurus hermaphroditus*	Least Concern ver 3.1	1
Leopard cat	*Prionailurus bengalensis*	Least Concern ver 3.1	2
Large Indian civet	*Viverra zibetha*	Near Threatened ver 3.1	2
Small Indian civet	*Viverricula indica*	Least Concern ver 3.1	1
Chiroptera			
Lesser short-nosed fruit bat	*Cynopterus brachyotis*	Least Concern ver 3.1	2
Greater short-nosed fruit bat	*Cynopterus sphinx*	Least Concern ver 3.1	1
Great roundleaf bat	*Hipposideros armiger*	Least Concern ver 3.1	2
Bicolored roundleaf bat	*Hipposideros bicolor*	Least Concern ver 3.1	2
Intermediate roundleaf bat	*Hipposideros larvatus*	Least Concern ver 3.1	2
Indian pipistrelle	*Pipistrellus coromandra*	Least Concern ver 3.1	2
Intermediate horseshoe bat	*Rhinolophus affinis*	Least Concern ver 3.1	1
Leschenault’s rousette	*Rousettus leschenaultii*	Least Concern ver 3.1	1
Black-bearded tomb bat	*Taphozous melanopogon*	Least Concern ver 3.1	2
Theobald's tomb bat	*Taphozous theobaldi*	Least Concern ver 3.1	1
Pholidota			
Sunda pangolin	*Manis javanica*	Endangered A2d+3d+4d ver 3.1	1
Primates			
[Gibbon sp.]	*Hylobates* [*Nomascus*] sp.		6, 7
[Stump-tailed macaque]	*[Macaca arctoides]*	Vulnerable A3cd+4cd ver 3.1	3
[Crab-eating macaque subsp.]	*Macaca fascicularis validus*	Least Concern ver 3.1	6
Rhesus macaque	*Macaca mulatta*	Least Concern ver 3.1	2
Pygmy [slow] loris	*Nycticebus pygmaeus*	Vulnerable A2cd ver 3.1	2
Red-shanked douc [langur]	*Pygathrix nemaeus*	Endangered A2cd+3cd+4cd ver 3.1	2
Rodentia			
Asiatic brush-tailed porcupine	*Atherurus macrourus*	Least Concern ver 3.1	1
Pallas squirrel	*Callosciurus erythraeus*	Least Concern ver 3.1	1
Asian red-cheeked squirrel	*Dremomys rufigenis*	Least Concern ver 3.1	1
Long-tailed giant rat	*Leopoldamys sabanus revertens*	Least Concern ver 3.1	1
Indochinese maxomys	*Maxomys moi*	Least Concern ver 3.1	1
Asian white-bellied rat	*Niviventer bukit*		2

Chestnut white-bellied rat	*Niviventer fulvescens huang*	Least Concern ver 3.1	1
Sikkim forest rat	*Rattus andamanensis*	Least Concern ver 3.1	2
Rice-field rat	*Rattus argentiventer*	Least Concern ver 3.1	2
Yellow-chested rat	*Rattus flavipectus*		2
Brown rat	*Rattus norvegicus*	Least Concern ver 3.1	1
[Oriental houserat subsp.]	*Rattus tanezumi molliculus*	Least Concern ver 3.1	1
[Tanezumi rat subsp.]	*Rattus tanezumi germaini*	Least Concern ver 3.1	2
Cambodian striped squirrel	*Tamiops rodolphii*	Least Concern ver 3.1	1
Scandentia			
Northern treeshrew	*Tupaia belangeri*	Least Concern ver 3.1	4
Common treeshrew	*Tupaia glis*	Least Concern ver 3.1	1
Soricomorpha			
Asian house shrew	*Suncus murinus*	Least Concern ver 3.1	2
[Shrew sp.]	*Suncus* sp.		4

Appendix 6. Plants

Family and Common name	Species	IUCN listing	Source
Anthophyta - Dicotyledonae			
Acanthaceae			
	Dicliptera javanica Nees		2
	Hygrophila phlomoides Nees		2
	Justicia balansae Lindau		2
	Justicia glomerulata R. Ben.		2
	Phaulopsis parviflora Willd.		2
	Phlogacanthus annamensis R. Ben.		2
	Staurogyne debilis (T. Anderson) C.B. Clarke ex Merr.		2
	Staurogyne neesii (Vidal) C.B. Clarcke ex Merr.		2
	Strobilanthes anamitica Kuntze		2
	Strobilanthes longipedunculata Terao		2
Sweet clock vine	*Thunbergia fragrans* Roxburgh var. *heterophylla* Clark		2
	Thunbergia geoffrayi R. Ben.		2
Aizoaceae			
Shoreline seapurslane	*Sesuvium portulacastrum* (L.) L.		2
Amaranthaceae			
Prickly chaff flower	*Achyranthes aspera* L.		2
Sessile joyweed	*Alternanthera sessilis* (L.) R. Brown ex de Candolle		2
Spiny amaranth	*Amaranthus spinosus* L.		2
Green amaranth	*Amaranthus viridis* L.		2
Plumed cockscomb	*Celosia argentea* L.		2
Pastureweed	*Cyathula prostrata* (L.) Bl.		2
Anacardiaceae			
	Buchanania lucida Bl.		2
	Buchanania siamensis Miq.		2
	Gluta tavoyana Wall. ex Hook.f.		2
	Gluta wrayi King		2
Marking nut	*Semecarpus anacardiopsis* Evr. et Tard.		2
	Semecarpus caudata Pierre		2
	Semecarpus reticulata Lec.		4
Ancistrocladaceae			
	Ancistrocladus cochinchinensis Gagnep..		2
	Ancistrocladus tectorius (Lour.) Merr.		2
	Ancistrocladus wallichii Planch.		2
Annonaceae			
	Alphonsea gaudichaudiana (Baill.) Finet & Gagnep..		2

	Artabotrys vinhensis Ast		2
	Dasymaschalon lomentaceum Finet & Gagnep..		2
Saaiyut	*Desmos chinensis* Lour.		2
Dwarf Ylang Ylang shrub	*Desmos cochinchinensis* Lour.		2
	Desmos dinhensis (Pierre ex Finet & Gagnep..) Merr.		2
	Desmos pedunculosus (A.DC.) Bân		2
	Enicosanthellum plagioneurum (Diels) Bân	Least Concern ver 2011.2	2
	Fissistigma glaucescens (Hance) Merr.		2
	Fissistigma latifolium (Dunal) Merr.		2
	Friesodielsia fornicata (Roxb.) D.Das		2
	Goniothalamus gabriacianus (Baill.) Jovet-Ast		2
	Goniothalamus multiovulatus Ast		2
	Goniothalamus tamirensis Pierre ex Finet & Gagnep.		2
	Goniothalamus touranensis Ast		2
Pulithal	*Goniothalamus wightii* J. Hk. & Thomas		2
Vú bò đà nẵng	*Mitrella touranensis* Bân		2
Tháp hình mềm	*Orophea mollis* (Pierre) Bân		2
	Orophea sp.		2
	Polyalthia clemensorum Ast & Jovet		2
	Polyalthia corticosa (Pierre) Finet & Gagnep.		2
	Polyalthia jenkinsii Hk. f. & Thoms		2
	Polyalthia suberosa (Roxburgh) Thwaites		2
	Uvaria cordata (Dunal) Alston		2
	Uvaria fauveliana Pierre ex Ast		2
	Uvaria hirsuta Jack		2
	Xylopia vielana Pierre		2
Apiaceae			
Centella coinwort	*Centella asiatica* L. Urban		2
Lawn marshpennywort	*Hydrocotyle sibthorpioides* Lamarck		2
Chinese celery	*Oenanthe javanica* (Bl.) DC.		2
Apocynaceae			
Blackboard tree	*Alstonia scholaris* (L.) R.Br.	Least Concern ver 2.3	2
	Alyxia annamensis Pit.		2
	Alyxia racemosa Pit.		2
Sea mango	*Cerbera mangas* L.		2
	Cleghornia malaccensis (Hook.f.) King et Gamble		4
	Melodinus annamensis Pit.		2

	Melodinus cochinchinensis (Lour.) Merr.		2
	Parsonsia laevigata (Moon) Alston		4
	Tabernaemontana bovina Lour.		2
	Wrightia annamensis Eberh. & Dubard		2
	Wrightia rubriflora Pit.		2
Aquifoliaceae			
	Ilex ficoidea Hemsl.		2
	Ilex godajam Colebr. ex Hook.f.		2
Kurogane holly	*Ilex rotunda* Thunberg in Murray		2
	Ilex wallichii Hook.f.		2
Araliaceae			
Cuồng đà nẵng	*Aralia touranensis* Ha		2
	Brassaiopsis glomerulata (Bl.) Regel		2
	Macropanax simplicifolius C.B.Shang		2
	Schefflera obovatifoliolata C.B.Shang		2
Ivy tree	*Schefflera octophylla* (Lour.) Harms.		2
	Schefflera quangtriensis C.B.Shang		2
Aristolochiaceae			
Indian birthwort	*Aristolochia tagala* Ludolf Karl Adelbert von Chamisso		2
Asclepediaceae			
Crown flower	*Calotropis gigantea* (Linn.) Aiton f.		2
	Hoya balansae Costantin		2
	Hoya diversifolia Bl.		2
	Marsdenia urceolata Decne.		2
	Streptocaulon griffithii Hook. f.		2
Asteraceae			
Billygoat-weed	*Ageratum conyzoides* L.		2
Beach wormwood	*Artemisia campestris* L. subsp. *maritima*		2
Sambong	*Bl.a balsamifera* (Linn.) DC.		2
Big-flowered Bl.a	*Bl.a megacephala* (Randeria) Chang et Tseng		2
False daisy	*Eclipta prostrata* (L.) L.		2
Lilac tasselflower	*Emilia sonchifolia* (L.) DC.		2
Christmas bush	*Eupatorium odoratum* L.		2
Okinawa spinach	*Gynura crepioides*		2
Balsamiinaceae			
	Impatiens claviger Hook.f.		2
Bóng nước đà nẵng	*Impatiens touranensis* Tardieu		2
Bignoniaceae			
	Dolichandrone serrulata (Wall. ex DC.) Seem		2
	Radermachera eberhardtii Dop		2
Golden tree jasmine	*Radermachera hainanensis* Merr.		2

Tree jasmine	*Radermachera ignea* (Kurz) Steenis		2
Boraginaceae			
Octopus bush	*Heliotropium foertherianum* Diane & Hilger (formerly *Argusia argentea* (L. f.) Heine)	Least Concern ver 2.3	2
	Carmona microphylla (Lam.) G. Don.		2
	Cordia glabra Chamisso		2
	Cordia grandis Roxb.		2
Narrow-leafed bird lime tree	*Cordia subcordata* Poir.	Least Concern ver 2.3	2
Indian heliotrope	*Heliotropium indicum* L.	Least Concern ver 3.1	2
	Heliotropium strigosum Willd.		2
Mountain tournefortia	*Tournefortia montana* Lour.		2
Buddlejaceae			
White butterfly bush	*Buddleja asiatica* Lour.		2
Burseraceae			
	Bursera serrata Wall.ex Colebr.		2
	Canarium subulatum Guillaumin		2
Cactaceae			
Prickly pear	*Opuntia cochenillifera* (L.) Salm-Dyck		2
Campanulaceae			
	Lobelia zeylanica L.		2
Asiatic bellflower	*Wahlenbergia marginata* (Thunb.) DC.		2
Capparaceae			
	Capparis acutifolia Sweet		2
	Capparis sepiara (L.) R.Br.		2
	Capparis thorelii Gagnep..		2
	Capparis zeylanica L.		2
Spiderwisp	*Cleome gynandra* L.		2
Asian spiderflower	*Cleome viscosa* L.		2
	Crateva magna (Lour.) DC.		2
Caprifoliaceae			
Large-flowered honeysuckle	*Lonicera macrantha* (D. Don). Spreng.		2
Sweet viburnum	*Viburnum odoratissimum* Ker Gawl.		2
Caryophyllaceae			
Common mouse-ear chickweed	*Cerastium fontanum* Baumg.		2
	Polycarpaea gaudichaudii Gagnep.		2
	Polycarpaea stylosa Gagnep.		2
	Polycarpon prostratum (Forssk.) Asch. & Schweinf.		2
Celastraceae			
	Celastrus annamensis Tardieu-Blot.		2

	Euonymus laxiflorus Champ. ex Ben.th.		2
	Euonymus mitratus Pierre		2
	Gymnosporia diversifolia Maxim.		2
	Gymnosporia mekongensis Pierre		2
	Gymnosporia tonkinensis Pit.		2
Chinese salacia	*Salacia chinensis* L.		2
	Salacia verrucosa Wight		2
	Salacia sp.		2
	Siphonodon celastrineus Griff.	Least Concern ver 2.3	2
Chloranthaceae			
Pearl orchid	*Chloranthus spicatus* (Thunb.) Makino		2
Combretaceae			
Chinese honeysuckle	*Quisqualis indica* L. var. *pierrei* (Gagnep..) O. Lecompte		4
Connaraceae			
	Cnestis palala (Lour.) Merr.		2
	Connarus cochinchinensis (Baill.) Pierre		2
	Connarus paniculatus Roxburgh		2
	Rourea acropetala Pierre		2
Kamagsa	*Rourea minor* (Gaertn.) Aubl.		2
	Rourea oligophlebia Merr.		2
Convolvulaceae			
	Aniseia harmandii (Gagn.) P.H.		4
	Argyreia argentea (Roxb.) Choisy		2
	Argyreia lanceolata Choisy		2
Blue morning glory	*Ipomoea indica* (Burm.) Merr.		2
	Ipomoea bonii Gagnep..		2
Pink morning glory	*Ipomoea carnea* Jacq. ssp. *fistulosa* (Mart. ex Choisy		2
	Ipomoea eberhardtii Gagnep.		2
Beach morning glory	*Ipomoea pes-caprae* (L.) R. Br.		2
African morning glory	*Xenostegia tridentata* (L.) D. F. Austin & Staples		2
Cucurbitaceae			
Lollypop climber	*Diplocyclos palmatus* (L.) C.Jeffrey		2
	Gymnopetalum integrifolium (Roxb.) Kurz.		2
	Solena amplexicaulis (Lam.) Gandhi		2
	Trichosanthes sp.		2
Dilleniaceae			
Dog teak	*Dillenia pentagyna* Roxb.		2
	Dillenia scabrella Roxb.		2
	Dillenia turbinata Finet & Gagnep.		2

	Tetracera sarmentosa (L.) Vahl subsp. *asiatica* (Lour.) Hoogl.		2
	Tetracera scandens Linn. Merr.		2
Dipterocarpaceae			
	Dipterocarpus baudii Korth.	Critically Endangered A1cd+2cd ver 2.3	2
	Dipterocarpus gracilis Bl.	Critically Endangered A1cd+2cd ver 2.3	2
Hollong	*Dipterocarpus retusus* Bl.	Vulnerable ver 2.3	2
	Dipterocarpus turbinatus C. F. Gaertner	Vulnerable ver 2.3	2
White thingan	*Hopea odorata* Roxb.	Vulnerable ver 2.3	2
White seraya	*Parashorea stellata* Kurz.	Critically Endangered A1cd, B1+2c ver 2.3	2
	Vatica mangachapoi Blanco subsp. *obtusifolia* (Elmer) P.S.Ashton	Endangered A1cd ver 2.3	2
Droseraceae			
Tropical sundew	*Drosera burmannii* Vahl		2
Indian sundew	*Drosera indica* L.		2
EBen.aceae			
	Diospyros apiculata Hiern	Least Concern ver 2.3	2
Philippine striped ebony	*Diospyros buxifolia* (Bl.) Hiern		2
	Diospyros cauliflora Bl.		2
Pale moon ebony	*Diospyros malabarica* (Desr.) Kostel.		2
Malaysian persimmon	*Diospyros maritima* Bl.		2
	Diospyros pendula Hasselt ex Hassk.		2
	Diospyros pilosula (A.DC.) Wall. ex Hiern.		2
	Diospyros salletii Lecomte		2
Elaeocarpaceae			
	Elaeocarpus floribundus Bl.		2
	Elaeocarpus griffithii (Wight) A.Gray		2
Hainan elaeocarpus	*Elaeocarpus hainanensis* Oliver		2
Elaeagnaceae			
	Elaeagnus conferta Roxb.		2
Erythroxylaceae			
	Erythroxylum annamense Tardieu		2
Euphorbiaceae			
Indian nettle	*Acalypha indica* L.		2
	Actephila daii Yhin		2
	Alchornea rugosa (Lour.) Müll. Arg.		2
Currant tree	*Antidesma bunius* (L.) Spreng		2
	Bridelia cambodiana Gagnep.		2

	Antidesma chonmon Gagnep.		2
	Antidesma cochinchinensis Gagnep.		2
Black currant tree	*Antidesma ghaesembilla* Gaertn.		2
	Antidesma hainanensis Merr.		2
	Antidesma paxii F.P.Metcalf		2
	Antidesma rec Gagnep.		2
Common aporosa	*Aporosa dioica* (Roxb.) Muell. Arg.		2
Burmese grape	*Baccaurea ramiflora* Lour.		2
	Baccaurea sylvestris Lour.		4
Bishop wood	*Bischofia javanica* Bl.		2
Waxy leaf	*Breynia fruticosa* (L.) Hook.f.		2
	Breynia grandiflora Beille		2
	Breynia rostrata Merr.		2
	Breynia septata Beille		2
Makaa	*Bridelia ovata* Decne		2
	Bridelia parvifolia Kuntze		2
Pop-gun seed	*Bridelia tomentosa* Bl.		2
	Claoxylon hainanensis Pax et Hoffm		2
	Claoxylon indicum (Reinw. ex Bl.) Hassk.		4
	Claoxylon longifolium (Bl.) Endl. ex Hassk.		2
	Cleistanthus eberhardtii (Gagnep..) Croizat		2
Chonoo	*Croton argyratus* Bl.		2
	Croton caryocarpus Croizat		2
Vente conmigo	*Croton glandulosus* L.		2
Kowli seeds	*Croton joufra* Roxburgh		2
	Croton kongensis Gagnep.		2
	Croton maieuticus Gagnep.		2
Oblong-leaved croton	*Croton oblongifolius* Roxb.		2
	Croton phuquocensis Croizat	Vulnerable ver 2.3	2
	Croton potabilis Croizat		2
	Croton roxburghianus Bal.		2
Plaudeang	*Croton thorelii* Gagnep.		2
	Croton touranensis Gagnep.	Vulnerable ver 2011.2	2
	Epiprinus poilanei Gagnep..		2
	Erismanthus obliquus Wall. ex Müll.Arg		2
Antique euphorbia	*Euphorbia antiquorum* L.		2
Asthma weed	*Euphorbia hirta* L.		2
Thyme-leaf spurge	*Euphorbia thymifolia* L.		2
	Flueggea jullienii (Beille) G.L.Webster		4
	Glochidion annamense Beille		2

Thick-leaved abacus plant	*Glochidion hirsutum* (Roxb.) Voigt.		2
Monkey apple	*Glochidion littorale* Bl.		2
	Glochidion velutinum Wight.		4
	Macaranga andamanica Kurz		2
	Macaranga trichocarpa (Reichb. & Zoll.) Műll.Arg.		2
White-back-leaf mallotus	*Mallotus apelta* (Lour.) Müll. Arg.		2
Barbate mallotus	*Mallotus barbatus* Müll.Arg.		2
	Mallotus floribundus (Bl.) Műll.Arg.		2
	Mallotus oblongifolius (Miq.) Müll. Arg.		2
Panicled mallotus	*Mallotus paniculatus* (Lam.) Müll. Arg.		2
Red kamala	*Mallotus philippensis* Muell.		2
	Oligoceras eberhardtii Gagnep.		2
	Phyllanthus annamensis Beille		2
Potato plant	*Phyllanthus reticulatus* Poir.		2
	Phyllanthus ruber (Lour.) Spreng.		2
	Phyllanthus rubescens Beille		2
	Phyllanthus touranensis Beille		2
Shatterstone	*Phyllanthus urinaria* L.		2
	Sapium cochinchinensis (Lour.) Kuntze		2
Chinese tallow tree	*Sapium sebiferum* (L.) Roxb		2
	Breynia glauca Craib		2
	Sauropus stipitatus Hook.f.		2
	Trigonostemon gaudichaudii (Baill.) Müll.Arg.		2
	Trigonostemon kwangsiensis Hand.-Mazz		2
	Trigonostemon thyrsoides Stapf.		2
	Tritaxis gaudichaudii Baill.		2
Fagaceae			
	Castanopsis ceratacantha Rehder & E.H.Wilson		2
White oak	*Castanopsis nebulosum* A. Camus		2
	Castanopsis nhatrangensis Hickel & A.Camus		2
	Castanopsis scortechinii Gamble	Vulnerable B1+2c ver 2.3	2
	Castanopsis tribuloides (Sm.) A. DC.		2
	Lithocarpus amygdalifolius (Skan) Hayata		2
	Lithocarpus annamensis (Hickel & A.Camus) Barnett		2
	Lithocarpus annamitorus (A.Chev.) A.Camus		4
	Lithocarpus bacgiangensis (Hickel & A. Camus) A. Camus		2

	Lithocarpus eleagnifolius Schott.		2
	Lithocarpus fenestratus (Roxb.) Rehder		2
	Lithocarpus gigantophyllus (Hickel & A.Camus) A.Camus		4
	Lithocarpus quangnamensis A.Camus		2
	Lithocarpus thomsonii (Miq.) Rehder		2
	Lithocarpus vestitus (Hickel & A.Camus) A.Camus		2
	Pasania ombrophila A.Camus		2
	Pasania scortechinii (King ex Hook.f.) A.Camus		2
	Quercus subumbilicata A.Camus		2
	Quercus thorelii Hickel & A. Camus		2
Flacourtiaceae			
	Casearia grewiaefolia Vent. var. *deglabrata* Koord. & Valeton		2
Governor's plum	*Flacourtia indica* (Burm. f.) Merr.		2
Coffee plum	*Flacourtia jangomas* (Lour.) Raeusch		2
Attak	*Flacourtia montana* Graham		4
Indian prune	*Flacourtia rukam* Zoll.et Morr.		2
	Homalium cochinchinense (Lour.) Druce		2
Chaulmoogra	*Hydnocarpus anthelmintica* Pierre ex Laness		2
	Hydnocarpus clemensorum Gagnep.		2
Mountain hydnocarpus	*Hydnocarpus ilicifolia* King		2
	Scolopia chinensis (Lour.) Clos		2
	Scolopia saeva (Hance) Hance		2
Gesneriaceae			
	Aeschynanthus poilanei Pellegrin		2
	Chirita eberhardtii Pellegr.		2
	Hemiboea poilanei Pellegr.		2
Guttiferae (Clusiaceae)			
	Calophyllum balansae Pit.		2
False-mamey	*Calophyllum calaba* L.		2
	Calophyllum dryobalanoides Pierre		2
	Calophyllum rugosum P.F.Stevens		2
	Calophyllum touranense Gagnep.. ex P.F.Stevens		2
Bastard garcinia	*Garcinia merguensis* Wight		2
	Garcinia morella (Gaertn.) Desr.		4
	Garcinia nigrolineata Planch. ex T. Anderson		2
	Garcinia oblongifolia Champion ex Ben.tham		2
	Garcinia oligantha Merr.		2

	Garcinia schefferi Pierre		2
False mangosteen	*Garcinia xanthochymus* Hook		2
Hamamelidaceae			
	Altingia siamensis Craib		2
Hernandiaceae			
	Illigera celebica Miquel		2
	Illigera rhodantha Hance var. *dunniana* (H. Léveillé) Kubitzki		2
Hypericaceae			
	Cratoxylon cochinchinensis Bl.		2
Pink mempat	*Cratoxylum formosum* (Jack) Dyer	Least Concern ver 2.3	2
	Cratoxylum maingayi	Least Concern ver 2.3	2
Icacinaceae			
	Gonocaryum lobbianum (Miers) Kurz		2
	Iodes cirrhosa Turcz.		2
Ixonanthaceae			
	Ixonanthes reticulata Jack		2
Juglandaceae			
	Engelhardia roxburghiana Wall.		2
	Engelhardia spicata Lesch ex Bl.		2
Labiatae			
	Acrocephalus indicus (Burm. f.) Kuntze		2
Indian catmint	*Anisomeles indica* (L.) Kuntze		2
	Gomphostemma javanica (Bl.) Ben.tham		2
	Gomphostemma lucidum Wall. ex Ben.th		2
	Gomphostemma niveum Hook.f.		2
Chan plant	*Hyptis suaveolens* (L.) Poit.		2
Common leucas	*Leucas aspera* (Willd) Link		2
Ceylon slitwort	*Leucas zeylanica* (L.) R.Br.		2
Rau mèo velteri	*Orthosiphon velterii* Doan.		2
	Pogostemon auricularius (L.) Hassk		2
	Pogostemon pumilus (Graham) Press		2
	Scutellaria cochinchinensis Briq.		2
Lauraceae			
	Actinodaphne pilosa (Lour.) Merr		2
	Beilschmiedia brevipetiolata Kosterm		2
	Beilschmiedia percoriacea C.K. Allen		2
	Cinnamomum argenteum Gamble		2
	Cinnamomum durifolium Kosterm		4
Cinnamon	*Cinnamomum iners* Reinw. ex Bl.		2
Selasian wood	*Cinnamomum parthenoxylon* (Jack) Meisn	Data Deficient ver 2.3	2
	Cinnamomum tonkinensis (Lecomte)		2

	A.Chev.		
	Cryptocarya chingii W.C.Cheng		2
	Cryptocarya hainanensis Merr.		2
	Dehaasia caesia Bl.		4
	Litsea cambodiana Lecomte		2
	Litsea citronella Kosterm		2
Mountain pepper	*Litsea cubeba* (Lour.) Pers.		2
	Litsea glutinosa (Lour.) C. Rob.		2
Kathang	*Litsea monopetala* (Roxb.) Persoon		2
Bời lời đỏ tươ	*Litsea salmonea* A. Chev.		4
	Litsea umbellata (Lour.) Merr.		4
	Litsea verticillata Hance		2
Scented machilus	*Machilus odoratissima* (Wall. ex Nees) var. *glabrata* Bl.		2
	Neolitsea elaeocarpa H.Liu		2
Lecythidaceae			
	Barringtonia coccinea (Lour.) Kostel		2
	Barringtonia macrostachya (Jack) Kurz		2
	Barringtonia musiformis King		2
Powder-puff tree	*Barringtonia racemosa* (L.) Spreng.		2
Leguminosae (Fabaceae): Caesalpinioideae			
	Bauhinia clemensiorum Merr.		2
Red trailing bauhinia	*Bauhinia coccinea* (Lour.) DC		2
	Bauhinia touranensis Gagnep..		2
Yellow nicker	*Caesalpinia bonduc* (L.) Roxb.		2
Gray nicker	*Caesalpinia crista* L.		2
	Caesalpinia latisiliqua (Cav.) Hattink		2
	Caesalpinia pubescens (Desf.) Hattink		2
	Cassia agnes (de Wit) Brenan		2
Sensitive partridge pea	*Cassia leschenaultiana* DC.		2
Coffee senna	*Cassia occidentalis* L.		2
Kassod tree	*Senna siamea* (Lam.) Irwin et Barneby		2
Golden senna	*Senna surattensis* (Burm. f.)		2
Sickle wild sensitive plant	*Senna tora* (L.) Roxb.		2
	Cynometra glomerulata Gagnep.		2
	Gleditsia australis F.B.Forbes & Hemsl.		2
	Peltophorum dasyrrhachis (Miq.) Kurz var. *tonkinense* (Pierre) K. Larsen & S. Larsen		2
	Sindora tonkinensis A.Chev. ex K.Larsen & S.S.Larsen	Data Deficient ver 2.3	2
Leguminosae (Fabaceae): Mimosoideae			
Sweet acacia	*Acacia farnesiana* (L.) Willd.		2

Climbing wattle	*Acacia pennata* (L.) Willd.		2
Red sandlewood	*Adenanthera pavonina* L. var. *microsperma* (Teijsm. & Binn.) I. C. Nielsen		2
	Albizia corniculata (Lour.) Druce.		2
Lebbeck tree	*Albizia lebbeck* (L.) Ben.th.		2
	Archidendron bauchei (Gagnep..) I.C.Nielsen		2
	Archidendron chevalieri (Kosterm.) I.C. Nielsen		4
Saint Thomas bean	*Entada phaseoloides* (L.) Merr.		2
White leadtree	*Leucaena leucocephala* (Lam.) de Wit		2
Giant sensitive plant	*Mimosa invisa* C. Wright		2
Sensitive plant	*Mimosa pudica* L.		2
Madras thorn	*Pithecellobium dulce* (Roxb.) Ben.th.		2
Leguminosae (Fabaceae): Papilionoideae			
Crab's eye	*Abrus precatorius* L.		2
Shyleaf	*Aeschynomene americana* L.		2
Indian jointvetch	*Aeschynomene indica* L.		2
White moneywort	*Alysicarpus vaginalis* (L.) DC.		2
Wild kulthi	*Atylosia scarabaeoides* (L.) Ben.th.		2
Pigeonp pea	*Cajanus cajan* (L.) Millsp.		2
Jackbean	*Canavalia cathartica* Thouars.		2
	Canavalia lineata (Thunb.) DC.		2
	Clianthus scandens (Lour.) Merr.		2
	Crotalaria albida Heyne ex Roth		2
	Crotalaria chinensis L.		2
Tiny rattlepod	*Crotalaria nana* Burm. f.		2
Smooth rattlebox	*Crotalaria pallida* Aiton		2
	Crotalaria phyllostachya Gagnep..		2
Rattleweed	*Crotalaria retusa* L.		2
	Crotalaria uncinella Lam.		2
Burmese rosewood	*Dalbergia bariensis* Pierre	Endangered A1cd ver 2.3	2
	Dalbergia pinnata (Lour.) Prain		2
	Dendrolobium triangulare (Retz.) Schindl.		2
Sal leaved desmodium	*Desmodium gangeticum* (L.) DC.		2
Carpon desmodium	*Desmodium heterocarpon* (L.) DC		2
Variable vagina wort	*Desmodium heterophyllum* (Willd.) DC.		2
Many-flowered desmodium	*Desmodium multiflorum* DC.		2
	Desmodium rubrum (Lour.) DC.		2
Tick clover	*Desmodium triflorum* (L.) DC.		2

	Dunbaria glabra Thuan		2
	Dunbaria nivea Miq.		2
	Dunbaria subrhombea (Miq.) Hemsl.		2
Purple coraltree	*Erythrina fusca* Lour.		2
	Flemingia macrophylla (Willd.) Merr.		2
Wildhops	*Flemingia strobilifera* (L.) W. T. Aiton		2
Hairy indigo	*Indigofera hirsuta* L.		2
	Indigofera nummularifolia (L.) Liv. ex Alston		2
Creeping indigo	*Indigofera spicata* Forssk.		2
Wild indigo	*Indigofera suffruticosa* P. Mill.		2
	Millettia eberhardtii Gagnep..		2
	Millettia pachyloba Drake		2
	Ormocarpum cochinchinense (Lour.) Merr.		2
	Ormosia pinnata (Lour.) Merr.		2
	Ormosia semicastrata Hance		2
	Ormosia sumatrana (Miq.) Prain		4
	Phyllodium elegans (Lour) Desv.		2
Tropical kudzu	*Pueraria phaseoloides* (Roxb.) Ben.th.		2
	Pueraria thomsonii Ben.th.		2
	Rothia indica (L.) Druce.		2
	Smithia conferta Smith.		2
Vietnamese sophora root	*Sophora tonkinensis* Gapnep.		2
	Spatholobus parviflorus (Roxb. ex DC.) Kuntze		2
	Tadehagi triquetrum (L.) H. Ohashi		2
Fishpoison	*Tephrosia purpurea* (L.) Pers.		2
Mung bean	*Vigna radiata* (L.) Wilczek var. *glabra* (Roxb.) Verde		2
Zombi pea	*Vigna vexillata* (L.) A.Rich.		2
	Zornia cantoniensis Mohlenb.		2
Loganiaceae			
	Mitrasacme pygmaea R.Br.		2
	Strychnos angustiflora Ben.th		2
	Strychnos dinhensis Pierre ex Dop		4
	Strychnos lucida R.Br.		2
	Strychnos ovata A.W. Hill		2
Loranthaceae			
	Helixanthera cylindrica (Jack ex Roxb.) Danser		2
	Helixanthera parasitica Lour.		2
	Taxillus balansae (Lecomte) Danser		2
	Taxillus chinensis (DC.) Danser.		2
Leafless mistletoe	*Viscum articulatum* Burm.f		2

	Viscum ovalifolium Wall ex DC		2
Lythraceae			
	Lagerstroemia crispa Pierre ex Laness.		2
Magnoliaceae			
Clemens magnolia	*Magnolia clemensiorum* Dandy		2
	Magnolia eriosepta (Dandy) Gagnep..		2
	Magnolia fistulosa (Finn. et Gagn.) Dandy		2
	Michelia faveolata Merr. ex Dandy		2
Malpighiaceae			
	Aspidopterys tomentosa (Bl.) A.Juss.		4
Malvaceae			
	Abutilon crispum (L.) Sweet		2
Indian mallow	*Abutilon indicum* (Linn.) Sweet.		2
	Hibiscus grewiaefolius Hassk.		2
Sea hibiscus	*Hibiscus tiliaceus* L.		2
Threelobe false mallow	*Malvastrum coromandelianum* (L.) Garcke		2
Heartleaf fanpetals	*Sida cordata* (Burm.f.) Borss.		2
Country mallow	*Sida cordifolia* L.		2
Arrowleaf sida	*Sida rhombifolia* L.		2
Ceaser's weed	*Urena lobata* L.		2
Melastomataceae			
	Blastus borneensis Cogn. ex Boerl. var. *eberhardtii* (Guillaumin) C.Hansen		2
	Diplectria barbata (Wall. ex C.B. Clarke) Franken & Roos		2
Hairy melastome	*Melastoma eberhardtii* Guillaumin		2
Himalayan melastome	*Melastoma normale* D. Don		2
	Melastoma orientale Guillaumin		2
	Melastoma paleaceum Naudin		2
Fox-tongued melastoma	*Melastoma sanguineum* Sims		2
	Melastoma septennervium (Lour.) Merr		2
Kaayam	*Memecylon edule* Roxb.		2
	Memecylon elegans Kurz		2
	Memecylon ligustrinum Naudin		2
Graceful memecylon	*Memecylon scutellatum* (Lour.) Hook. & Arn.		2
Ironwood	*Memecylon umbellatum* Burm.f.		2
	Osbeckia chinensis L.		2
	Osbeckia zeylanica DC. ex Naudin		2
	Phyllagathis driessenoudes Hansen	(I am unable to confirm species existence)	2

	Poilannammia trimera C.Hansen		2
	Vietsenia poilanei C.Hansen		2
	Vietsenia scaposa C. Hansen		2
Meliaceae			
	Aglaia littoralis Zippelius ex Miq.		2
	Dysoxylum cauliflorum Hiern.		4
	Dysoxylum cyrtobotryum Miq.		4
Maota mamala	*Dysoxylum samoense* A. Gray		4
	Trichilia connaroides (Wight & Arnott) Ben.tvelzen		4
Menispermaceae			
	Coscinium fenestratum (Gaertn.) Colebr		2
	Fibraurea recisa Pierre		2
	Limacia scandens Lour.		2
	Stephania hernandiifolia (Willd.) Walp.		2
	Tinomiscium petiolare Hook. f. & Thoms.		2
Molluginaceae			
	Gisekia pharnaceoides L.		2
Bitter cumin	*Glinus oppositifolius* (L.) Aug.DC		2
Mollugo	*Mollugo pentaphylla* Linn.		2
Moraceae			
	Artocarpus gomezianus Wall. ex Trecul		2
	Artocarpus melinoxylus Gagnep.		2
	Artocarpus nitidus Trécul ssp. *lingnanensis* (Merr.) F.M. Jarrett		2
	Artocarpus rigidus Bl. ssp. *asperulus* (Gagnep.) F.M.Jarrett		2
	Artocarpus styracifolius Pierre		2
Paper mulberry	*Broussonetia papyrifera* (L.) L'Her. ex Vent		2
Council tree	*Ficus altissima* Bl.		2
	Ficus annulata Bl.		2
Elephant ear fig tree	*Ficus auriculata* Lour.		2
Weeping fig	*Ficus Ben.jamina* L.		2
	Ficus callophylla Bl.		4
	Ficus callosa Willd.		2
Speakled leaf fig	*Ficus chartacea* Wallich ex King		2
	Ficus costata Aiton		2
	Ficus curtipes Corner		2
	Ficus depressa Bl.		2
	Ficus fistulosa Reinw. ex Bl.		2
	Ficus fulva Reinw. ex Bl.		2
Climbing stream fig	*Ficus heterophylla* L. f.		2
Kalapat tree	*Ficus heteropleura* Bl.		2

Wuzhimaotao	*Ficus hirta* Vahl.		2
	Ficus hispida L.f.		2
	Ficus ischnopoda Miq.		2
	Ficus lacor Buch.-Ham		2
	Ficus laevis Bl.		2
	Ficus lamponga Miq.		4
Langkok fig	*Ficus langkokensis* Drake		2
Curtain fig	*Ficus microcarpa* L.f.		2
	Ficus nervosa Heyne ex Roth		2
	Ficus phanrangensis Gagnep.		2
Climbing fig	*Ficus pumila* L.		2
	Ficus pyriformis Hook. & Arn.		2
Cluster fig tree	*Ficus racemosa* L.		2
Rumpf's fig tree	*Ficus rumphii* Bl.		2
	Ficus sagittata Vahl		4
	Ficus sarmentosa Buch.-Ham. ex Sm. var. *nipponica* (Franch. & Sav.) Corner		2
	Ficus sikkimensis Miquel		2
	Ficus simplicissima Lour. var. *annamica* (Gagnep..)		2
	Ficus stenophylla Hemsl.		2
	Ficus subcordata Bl.		4
	Ficus subulata Bl.		2
Sea fig	*Ficus superba* (Miq.) Miq. var. *japonica* Miq		2
Dye fig	*Ficus tinctoria Forst.* subsp. *gibbosa* (Bl.) Corner		2
	Ficus trichocarpa Bl. var. obtusa (Hasskarl) Corner		4
	Ficus tsjahela Burm. f.		2
	Ficus tuphapensis Drake		2
Starlight fig	*Ficus variegata* Bl.		2
White fig	*Ficus vasculosa* Wall. ex Miq.		2
Toothbrush tree	*Streblus asper* Lour.		2
	Streblus crenatus (Gagnep.) Corner		2
	Streblus ilicifolius (S. Vidal) Corner		2
	Streblus macrophyllus Bl.		2
Purple crow vine	*Trophis scandens* (Lour.) Hook. & Arn.		2
Moringaceae			
Drumstrick tree	*Moringa oleifera* Lam.		2
Myristicaceae			
	Knema elegans Warburg		2
	Knema furfuracea Warburg	Least Concern ver 3.1	2
	Knema mixta de Wilde	Vulnerable ver 2.3	2

	Knema pachycarpa de Wilde	Vulnerable ver 2.3	2
	Knema saxatilis de Wilde	Vulnerable ver 2.3	2
Myrsinaceae			
	Ardisia aciphylla Pit.		2
	Ardisia annamensis Pit.		2
	Ardisia calophylloides Pit.		2
	Ardisia cambodiana Pierre ex Pit.		2
	Ardisia capillipes Pit.		2
	Ardisia elegans Andrews		2
	Ardisia expansa Pit.		2
	Ardisia florida Pit.		2
Low shoebutton	*Ardisia humilis* Vahl.		2
	Ardisia incrassata Pit.		2
	Ardisia insignis Mez & Pittier		2
	Ardisia maxima Pit.		2
	Ardisia pseudopedunculosa Pit.		2
	Ardisia velutina Pit.		2
	Ardisia silvestris Pit.		2
False black pepper	*Embelia ribes* Burm.f.		2
	Embelia robusta Roxb.		2
	Maesa membranacea A. DC.		2
	Maesa perlarius (Lour.) Merr.		2
	Maesa ramentacea (Roxb.) A. DC.		2
	Maesa subdentata A. DC.		2
	Rapanea capitellata (Wall.) Mez.		2
	Rapanea cochinchinensis (A. DC.) Mez		2
Myrtaceae			
	Cleistocalyx retinervius Merr. & L.M.Perry		2
	Decaspermum gracilentum (Hance) Merr. & Perry		4
Silky myrtle	*Decaspermum humile* (G.Don) A.J.Scott		4
	Psidium gaujava L.		2
Silver back	*Rhodamnia dumetorum* (DC.) Merr. & L.M.		2
Downy rose myrtle	*Rhodomyrtus tomentosa* (Aiton) Hassk.		2
	Syzygium bracteolatum (Wight) Masam.		2
	Syzygium bullockii (Hance) Merr. & L.M. Perry		2
Box-leaf syzygium	*Syzygium buxifolium* Hook. Et Arn.		2
Jambul	*Syzygium cumini* (L.) Skeels.		2
	Syzygium finetii (Gagnep.) Merr. & L.M.Perry		2
	Syzygium lineatum (Bl.) Merr. & Perry		4
	Syzygium polyanthum (Wight) Walp.		4

	Syzygium stictanthum Merr. & L.M.Perry		4
	Syzygium syzygioides (Miq.) Merr. & L.M.Perry		2
	Syzygium touranense Merr. & Perry		2
Spicate eugenia	*Syzygium zeylanicum* (L.) DC.		2
Nepenthaceae			
	Nepenthes smilesii Hemsl.	Data Deficient ver 2.3	2
Ochnaceae			
	Gomphia serrata (Gaertn.) Kanis	Least Concern ver 2.3	2
Olacaceae			
	Harmandia mekongensis Pierre		2
	Olax imbricata Roxb.		2
Oleaceae			
	Jasminum brevilobium A.DC.		2
	Jasminum lanceolaria Roxb.		2
	Jasminum longipetalum King & Gamble		2
	Jasminum longisepalum Merr.		2
	Jasminum nervosum Lour.		2
	Jasminum scandens (Retz.) Vahl		2
	Jasminum subtriplinerve Bl.		2
	Jasminum undulatum Ker Gawl.		2
	Osmanthus pedunculatus Gagnep.		2
Onagraceae			
Creeping water primrose	*Ludwigia adscendens* (L.) H.Hara		2
Seedbox	*Ludwigia hyssopifolia* (G. Don) Exell.		2
Raven primrose willow	*Ludwigia octovalvis* (Jacq.) Raven		2
False primrose	*Ludwigia perennis* L.		2
Opiliaceae			
	Opilia amentacea Roxb.		2
Oxalidaceae			
Creeping red woodsorrel	*Oxalis corniculata* L.		2
Passifloraceae			
	Adenia heterophylla (Bl.) Koord. var. *heterophylla*		2
	Passiflora cochinchinensis Spreng.		2
Blue passion flower	*Passiflora caerulea* L.		2
Fetid passion flower	*Passiflora foetida* L.		2
Piperaceae			
	Piper boehmeriifolium (Miq.) Wall. ex C. DC		2
Balinese long pepper	*Piper retrofractum* Trel. & Yunck.		2
Pittosporaceae			
	Pittosporum Merr.ianum Gowda		2

Plantaginaceae			
Asian plantain	*Plantago asiatica* L.		2
Polygalaceae			
	Polygala malesiana Adema		2
Polygonaceae			
	Polygonum barbatum L.		2
Chinese knotweed	*Polygonum chinense* L.		2
Proteaceae			
	Helicia cochinchinensis Lour.		2
	Helicia stenophylla Merr.		2
	Heliciopsis lobata (Merr.) Sleum.		2
	Heliciopsis terminalis (Kurz) Sleum		2
Ranunculaceae			
	Anemone sumatrana de Vriese		2
	Clematis granulata (Finet & Gagnep.) Ohwi		2
Rhamnaceae			
Bird plum	*Sageretia theezans* Brongn.		2
	Ziziphus laui Merr.		2
	Ziziphus oenoplia (L.) Mill.		2
Rosaceae			
	Photinia Ben.thamiana Hance var. *salicifolia* Cardot		2
Giant bramble	*Rubus alceifolius* Poir.		2
	Rubus cochinchinensis Tratt		2
Broad-leaf bramble	*Rubus moluccanus* L.		2
Rubiaceae			
	Canthium dicoccum (Gaertn.) Teys. & Binn.	Vulnerable A1c ver 2.3	2
	Canthium horridum Bl.		2
	Fagerlindia depauperata (Drake) Tirveng.		2
	Gardenia annamensis Pit.		2
	Gardenia sp.		2
	Hedyotis multiglomerulata (Pit.) P.H.Ho		2
	Hedyotis pinifolia Wall. ex G. Don		2
	Hedyotis pressa Pierre ex Pit.		2
Malayalam	*Ixora nigricans* R. Br. Wt. & Arn.		2
	Ixora pierrei Merr.		2
	Lasianthus cyanocarpus Jack		2
	Lasianthus eberhardtii Pit.		2
	Lasianthus hoaensis Pierre ex Pit.		2
	Lasianthus lecomtei Pit.		2
	Morinda parvifolia Bartl.		2
Common Indian mulberry	*Morinda umbellata* L.		2

	Mussaenda densiflora H.L. Li		2
	Neonauclea purpurea (Roxb.) Merr.		2
	Neonauclea sessilifolia (Roxb.) Merr.		2
	Pavetta chevalieri Bremek.		2
	Pavetta wallichiana Steud.		2
	Psychotria fleuryi Pit.		2
	Psychotria montana Bl.		2
	Psychotria oligoneura Pierre ex Pit.		2
	Psychotria ovoidea (Pierre ex Pit.) P.H.Ho		2
Wild coffee	*Psychotria rubra* (Lour.) Poir.		2
	Randia acuminatissima Merr.		2
	Randia oxyodonta Drake		2
	Randia spinosa (Thunb.) Bl.		2
	Randia uliginosa DC.		2
	Rothmannia encodon (K. Schum.)Brem.		2
	Tarenna baviensis (Drake) Pit.		2
	Timonius jambosella (Gaertn.) Thwaites.	Critically Endangered B1+2cd ver 2.3	2
	Wendlandia paniculata (Roxb.) DC.		2
	Wendlandia paedicalyx Pit.		2
Rutaceae			
	Acronychia pedunculata (L.) Miq.		2
	Clausena excavata Burm.f.		2
	Clausena indica (Dalz.) Oliver		2
Wampee	*Clausena lansium* (Lour.) Skeels		2
	Evodia calophylla Guill.		2
	Evodia crassifolia Merr.		2
	Evodia meliaefolia (Hance) Ben.th		2
	Evodia sutchuenensis Dode		2
	Glycosmis crassifolia Ridl.	Critically Endangered B1+2c ver 2.3	2
	Glycosmis ovoidea Pierre		2
Orangeberry	*Glycosmis pentaphylla* (Retz.) Correa		2
	Glycosmis sapindoides Lindl. ex Oliv.		2
	Luvunga nitida Pierre		2
	Macclurodendron oligophlebia (Merr.) Hartl.		2
	Micromelum hirsutum Oliv.		2
	Murraya glabra (Guillaumin) Swingle		2
Orange jasmine	*Murraya paniculata* (L.) Jack		2
	Paramignya armata Oliv. var *andamanica* King		2

	Paramignya monophylla Wight		2
Prickly ash	*Zanthoxylum avicennae* (Lam.) DC.		2
Thorny ivy-rue	*Zanthoxylum myriacanthum* Wallich ex Hook.f.		2
	Zanthoxylum nitidum (Roxb.) DC		2
Sabiaceae			
	Meliosma lepidota Bl. ssp *longipes* (Merr.)		2
	Meliosma spathulata J.E.Vidal		2
Santalaceae			
	Scleropyrum wallichianum (Night & Arn.) Arn.	Least Concern ver 2.3	2
Sapindaceae			
	Allophylus brachypetalus Gagnep..		2
	Allophylus longifolius Radlk.		2
	Amesiodendron chinense (Merr.) Hu	Near Threatened ver 2.3	2
	Arytera littoralis Bl.	Least Concern ver 2.3	2
Ballon vine	*Cardiospermum halicacabum* L.		2
Hopbush	*Dodonaea viscosa* Jacq.		2
	Lepisanthes amplifolia (Pierre) Leenh.		2
	Lepisanthes fruticosa (Roxb.) Leenh.		2
	Lepisanthes rubiginosa (Roxb.) Leenh.		2
	Mischocarpus pentapetalus (Roxb.) Radlk.		2
Red pear fruit	*Mischocarpus sundaicus* Bl.		2
Wild rambutan	*Nephelium melliferum* Gagnep.		2
	Paranephelium spirei Lecomte		4
Island lychee	*Pometia pinnata* Forster & Forster f.		2
Sapotaceae			
	Madhuca cochinchinensis (Pierre ex Dubard) H.J.Lam		2
Peanut madhuca	*Madhuca subquincuncialis* H.J.Lam		2
Palu	*Manilkara hexandra* (Roxb.) Dubard		2
	Palaquium annamense Lecomte		
	Planchonella clemensii (Lecomte) P.Royen		2
Northern yellow boxwood	*Pouteria obovata* (R.Br.) Pierre		2
	Xantolis maritima (Pierre ex Dubard) P.Royen		2
Saxifragaceae			
Blue evergreen hydrangea	*Dichroa febrifuga* Lour.		2
Scrophulariaceae			
	Adenosma annamensis T.Yamaz		2
Water hyssop	*Bacopa monnieri* L. Pennell		2

	Buchnera cruciata Buch.-Ham. ex D. Don		2
	Centranthera tranquebarica (Spreng.) Merr.	Least Concern ver 3.1	2
Horsefly's eyes	*Dopatrium junceum* (Roxb.) Buch.-Ham		2
Mudmats	*Glossostigma diandrum* (L.) Kuntze		2
Finger grass	*Limnophila chinensis* (Osbeck) Merr.	Least Concern ver 3.1	2
Indian marshweed	*Limnophila indica* (L.) Druce	Least Concern ver 3.1	2
	Limnophila laxa Ben.th.	Least Concern ver 2011.2	2
	Limnophila micrantha Ben.th.	Least Concern ver 3.1	2
Dwarf ambulia	*Limnophila sessiliflora* (Vahl) Bl.	Least Concern ver 3.1	2
	Lindernia anagallis (Burm. f.) Pennell	Least Concern ver 3.1	2
Fringed false pimpernel	*Lindernia ciliata* (Colsmann) Pennell	Least Concern ver 3.1	2
Malayan false pimpernel	*Lindernia crustacea* (L.) F.Muell	Least Concern ver 3.1	2
	Lindernia micrantha D.Don	Least Concern ver 3.1	2
	Lindernia mollis (Ben.th.) Wettst	Least Concern ver 3.1	2
	Lindernia oblonga (Ben.th.) Merr. & Chun		2
	Lindernia stolonifera T.Yamaz.		2
Licorice weed	*Scoparia dulcis* L.		2
	Torenia Ben.thamiana Hance		2
	Torenia poilanei Bonati		2
Simaroubaceae			
Bitter charm	*Eurycoma longifolia* Jack ssp *longifolia*		2
	Harrisonia perforata (Blanco) Merr.		2
	Picrasma javanica Bl.		2
Solanaceae			
Glossy nightshade	*Solanum americanum* Mill.		2
Indian nightshade	*Solanum lasiocarpum* Dunal		2
	Solanum thruppii C.H. Wright		2
Sterculiaceae			
	Helicteres angustifolia L. var. obtusa (Wall. ex Kurz) Pierre		2
	Helicteres lanceolata A.DC.		2
	Heritiera cochinchinensis Kost.		2
Looking-glass mangrove	*Heritiera littoralis* Dryand.	Least Concern ver 3.1	2

Large-leaf looking-glass mangrove	*Heritiera macrophylla* Wall. ex Kurz		2
	Pterospermum heterophyllum Hance.		2
	Pterospermum jackianum Wall.		2
	Pterospermum megalocarpum Tardieu		2
	Sterculia cochinchinensis Pierre		2
Lance-leaved sterculia	*Sterculia lanceolata* Cav.		2
Styracaceae			
	Styrax agrestis (Lour.) G. Don		2
Gum benjamin tree	*Styrax benzoin* Dryand.		4
Symplocaceae			
	Symplocos adenophylla Wall. ex G.Don var *adenophylla*		2
	Symplocos adenophylla Wall. & G.Don var. *touranensis* (Guillaumin) Noot		2
	Symplocos cochinchinensis (Lour.) S.Moore ssp. *laurina* (Retz.) Noot		2
	Symplocos henscheli ssp. *henscheli* (Mor.) Clarke		2
	Symplocos hookeri C.B. Clarke		2
	Symplocos sumuntia Buch.-Ham. ex D. Don.		2
	Symplocos viridissima Brand		2
Theaceae			
	Camellia caudata Wall.		2
	Camellia gaudichaudii (Gagnep..) Sealy		2
White wine	*Eurya japonica* Thunb.		2
	Gordonia balansae (Pitard) Hu.		2
Thymelaeaceae			
	Aquilaria baillonii Pierre ex Lecomte		2
	Linostoma decandrum (Roxb.) Wall, ex Meissn		2
Bootlace bush	*Wikstroemia indica* (L.) C. A. Mey.		2
Tiliaceae			
	Brownlowia tabularis Pierre		2
	Colona sp.		2
Phasla	*Grewia asiatica* L.		2
	Grewia astropetala Pierre		2
	Grewia bulot Gagnep.		2
	Grewia celtidifolia Juss.		2
	Grewia eberhardtii Lecomte		2
	Grewia laurifolia Hook. ex Mast.		2
	Grewia paniculata Roxb.		2
	Grewia polygama Roxb.		2
	Triumfetta bartramia L.		2

	Triumfetta grandidens Hance		2
	Triumfetta pseudocana Sprague & Craib		2
	Triumfetta repens (Bl.) Merr. & Rolfe		2
Ulmaceae			
Charcoal tree	*Trema orientalis* (L.) Bl.		2
Urticaceae			
	Poikilospermum annamense (Gagnep.) Merr.		2
Graceful pouzolzsbush	*Pouzolzia zeylanica* L.) Ben.n.		2
VerBen.aceae			
	Callicarpa acutidens Schauer		2
	Callicarpa albida Bl.		2
	Callicarpa bracteata Dop		2
	Callicarpa candicans (Burm. f.) Hochr.		2
	Callicarpa loureiri Hook. et Arn.		2
	Callicarpa nudiflora Hook. & Arn		2
	Callicarpa poilanei Dop		2
	Clerodendrum cochinchinense Dop		2
	Clerodendrum cyrtophyllum Turcz.		2
	Clerodendrum gaudichaudii Dop		2
Seaside clerodendrum	*Clerodendrum inerme* (L.) Gaertn		2
Kaempfers glorybower	*Clerodendrum kaempferi* (Jacq.) Siebold		2
Pagoda flower	*Clerodendrum paniculatum* L.		2
Cashmere bouquet	*Clerodendrum philippinum* Schauer var. *simplex* Moldenke		2
	Clerodendrum robinsonii Dop		2
Parrots beak	*Gmelina philippinensis* Cham		2
Spanish flag	*Lantana camara* L.		2
	Premna corymbosa (Burm.f.) Rottl. & Willd.		2
	Sphenodesma griffithiana Wight		2
	Sphenodesma involucrata (Presl) Robins		2
	Sphenodesma mollis Craib		2
Blue porterweed	*Stachytarpheta jamaicensis* (L.) Vahl		2
Common verBen.a	*VerBen.a officinalis* L.		2
Smooth chaste tree	*Vitex glabrata* R.Br.		2
Five leaved chaste tree	*Vitex negundo* L.		2
	Vitex peduncularis Wall. ex Schauer		2
	Vitex quinata (Lour.) F.N. Williams		2
Simple leaved chaste tree	*Vitex trifolia* L.		2
	Vitex tripinnata (Lour.) Merr.		2
Vitaceae			
	Ampelopsis cantoniensis (Hook. et Arn.) Planch.		2
	Cayratia geniculata (Bl.) Gagnep.		2

	Cayratia mollissima (Wall.) Gagnep.		2
	Cissus adnata Roxb.		2
	Leea bracteata C.B. Clarke		2
	Leea rubra Bl. ex Spreng		2
	Tetrastigma erubescens Planch. var. *monospermum* Gagnep.		2
	Tetrastigma gaudichaudianum Planch.		2
	Tetrastigma robinsonii Gagnep.		2
	Tetrastigma strumarium (Planch.) Gagnep.		2
	Tetrastigma touranense Gagnep.		2
	Vitis balansaeana Planch.		2
Anthophyta - Monocotyledonae			
Araceae			
	Alocasia longifolia Engl. & K.Krause		2
Giant taro	*Alocasia macrorrhizos* (L.) G.Don		2
	Anadendrum montanum (Bl.) Schott		2
	Epipremnum giganteum (Roxb.) Schott		2
Nampu	*Homalomena occulta* (Lour.) Schott		2
	Pothos angustifolius (Raf.) C.Presl.		2
	Pothos gigantipes Buchet ex P.C.Boyce		2
	Pothos penicilliger Gagnep.		2
	Pothos repens (Lour.) Druce		2
	Pothos touranensis Gagnep.		2
	Rhaphidophora chevalieri Gagnep.		2
	Rhaphidophora korthalsii Schott.		2
	Schismatoglottis cadieri Buchet & Gagnep.		2
Asparagaceae			
Wild asparagus	*Asparagus acerosus* Roxb.		2
	Asparagus cochinchinensis (Lour.) Merr.		2
	Asparagus gaudichaudianus Kunth		2
Dracaena	*Dracaena angustifolia* Roxb.		2
Dragon blood dracaena	*Dracaena cambodiana* Pierre ex Gagnep.		2
	Dracaena elliptica Thunb. & Dalm		2
Commelinaceae			
	Aclisia secundiflora (Bl.) Bakh. f.		2
Tropical spiderwort	*Commelina Ben.ghalensis* L.		2
Nabhali	*Cyanotis cristata* (L.) D. Don		2
	Cyanotis papilionacea (Burm.f.) Schult. & Schult.f.	Least Concern ver 2011.2	2
Climbing flower cup	*Floscopa scandens* Lour.		2
	Murdannia giganteum (Vahl) Brückner		2

Nakedstem dewflower	*Murdannia nudiflora* (L.) Brenan		2
Asiatic dewflower	*Murdannia spirata* (L.) Brückner		2
	Murdannia vaginata (L.) G. Brückner	Least Concern ver 3.1	2
	Pollia thyrsiflora (Bl.) Endl. ex Hassk.		2
Convallariaceae			
Japanese fairy bells	*Disporum trabeculatum* Gagnep.		2
Lilyturf	*Liriope graminifolia* (L.) Baker		2
	Ophiopogon caulescens (Bl.) Baker		2
Sparkler lilyturf	*Ophiopogon chingii* Wang et Tang		2
Aztec grass	*Ophiopogon intermedius* D. Don		2
	Ophiopogon longifolius Decne.		2
	Ophiopogon reptans Hook.f.		2
Cyperaceae			
Water grass	*Bulbostylis barbata (*Rottb.) C.B.Clarke		2
	Carex baccans Nees		2
	Carex commixta Steud.		2
	Carex maubertiana Boott		2
Poorland flatsedge	*Cyperus compressus* L.		2
Japanese flatsedge	*Cyperus javanicus* Houtt.		2
Purple nutsedge grass	*Cyperus rotundus* L.	Least Concern ver 3.1	2
	Cyperus tenuispica Steud.		2
	Fimbristylis argentea (Rottb.) Vahl	Least Concern ver 3.1	2
Globe fimbry	*Fimbristylis globulosa* Kunth.		2
	Fimbristylis lasiophylla J.Kern		2
Flatspike sedge	*Fimbristylis ovata* (Burm.f.) Kern	Least Concern ver 3.1	2
	Fimbristylis sericea (Poir.) R. Br.		2
Yefen	*Fuirena umbellata* Rottbøll	Least Concern ver 3.1	2
	Gahnia baniensis Ben.l		2
	Hypolytrum nemorum (Vahl) Spreng.		2
Whitehead spikesedge	*Kyllinga nemoralis* (J.R. Forst. & G. Forst.) Dandy ex Hutch. & Dalziel.		2
	Mariscus dregeanus Kunth		2
	Scirpus annamicus Raymond		2
	Scirpus lateriflorus J. F. Gmel.		2
Nutrush	*Scleria ciliaris* Nees		2
	Scleria levis Retz.		2
	Scleria oblata S.T.Blake ex J.Kern		2
	Scleria terrestris (L.) Fassett.		2
	Scleria tonkinensis C. B. Clarke		2
Dioscoreaceae			

	Dioscorea dissimulans Prain & Burkill		2
Flagellariaceae			
Whip vine	*Flagellaria indica* L.		2
Hypoxidaceae			
	Curculigo annamitica Gagnep.		2
	Curculigo conoc Gagnep.		2
	Curculigo disticha Gagnep.		2
Melanthiaceae			
Flame lily	*Gloriosa superba* L.		2
Musaceae			
Scarlet banana	*Musa coccinea* Andrews		2
Orchidaceae			
	Acriopsis emarginata D.L.Jones & M.A.Clem.		2
	Aerides odorata (Poir.) Lour		2
Bamboo orchid	*Arundina bambusifolia* Lindl.		2
	Bulbophyllum insulsum (Gagnep.) Seidenf.		2
	Cheirostylis cochinchinensis Bl.		2
Aloe-leafed cymbidium orchid	*Cymbidium aloifolium* (L.) Sw.		2
Finlayson's cymbidium orchid	*Cymbidium finlaysonianum* Wall. ex Lindl.		2
	Cymbidium sp.		2
	Dendrobium aloifolium (Bl.) Rchb. f.		2
Small lipped dendrobium	*Dendrobium linguella* Rchb. f.		2
Terminal dendrobium	*Dendrobium terminale* Par. et Rchb. f.		2
	Doritis pulcherrima Lindl.		2
	Eria paniculata Lindl.		2
	Geodorum densiflorum (Lam.) Schltr.		2
	HaBen.aria viridiflora (Rottler ex Sw.) Lindl.		2
	Nervilia crispata (Bl.) Schltr. ex Kraenzl.		2
	Nervilia prainiana (King & Pantl.) Seidenf.		2
	Oberonia flacata King & Pantl.		2
	Podochilus intermedius Aver.		2
Palmae (Arecaceae)			
Sugar palm	*Arenga pinnata* (Wurmb) Merr.		2
	Calamus bousingonii Pierre		2
Osier-like rattan palm	*Calamus rudentum* Lour.		2
	Calamus salicifolius Becc.		2
	Calamus tetradactylus Hance		2
	Calamus tonkinensis Becc.		2
Fish-tail plam	*Caryota mitis* Lour.		2

	Caryota sympetala Gagnep.		2
	Daemonorops geniculatus Mart.		2
	Daemonorops pierreanus Becc.		2
	Licuala hexasepala Gagnep.		2
Mangrove date palm	*Phoenix paludosa* Roxb.	Near Threatened ver. 3.1	2
Pandanaceae			
	Freycinetia webbiana Gaudich.		2
	Pandanus humilis Lour.		2
	Pandanus tonkinensis Martelli ex B.C.Stone		2
Sikkim screw palm	*Pandanus urophyllus* Hance		2
Poaceae			
	Brachiaria ramosa (L.) Stapf.		2
Golden Ffalse beardgrass	*Chrysopogon aciculatus* (Retz.) Trin.		2
Dog's tooth grass	*Cynodon dactylon* (L.) Pers.		2
Indian crabgrass	*Digitaria longiflora* (Retz.) Pers.		2
	Digitaria quinhonensis A.Camus		2
Blady grass	*Imperata cylindrica* (L.) P. Beauv.		2
Tight-flowered scrambling bamboo	*Melocalamus compactiflorus* (Kurz) Ben.th.		2
Seashore paspalum	*Paspalum vaginatum* Sw.		2
	Phragmites vallatoria (Pluk. ex L.) Veldkamp		2
Rose natal grass	*Melinis repens* (Willd.) Zizka		2
	Schizostachyum zollingeri Steud.		2
Tiger grass	*Thysanolaena maxima* (Roxb.)		2
Vetiver grass	*Vetiveria nemoralis* (Balansa) A. Camus		2
Smilacaceae			
	Heterosmilax gaudichaudiana (Kunth) Maxim.		2
	Smilax bauhinioides Kunth		2
Sarsaparilla	*Smilax china* f. obtusa H. Léveillé		2
	Smilax corbularia Kunth		2
China root	*Smilax glabra* Roxb.		2
	Smilax lanceifolia Roxb.		2
	Smilax menispermoidea D.C.		2
	Smilax perfoliata Lour.		2
	Smilax poilanei Gagnep.		2
Stemonaceae			
	Stemona tuberosa Lour.		2
Xyridaceae			
Feathered yellow-eye	*Xyris complanata* R.Br.		2
	Xyris pauciflora Willd.		2

Zingiberaceae			
Garden ginger	*Alpinia chinensis* (Retz.) Roscoe		2
Blue ginger	*Alpinia galanga* (L.) Willd.		2
	Amomum trilobum Gagnep.		2
	Stahlianthus campanulatus Kuntze		2
Coniferophyta - Gymnospermae			
Cycadaceae			
Forest cycad	*Cycas pectinata* Buch.-Ham.	Vulnerable A2c ver 3.1	2
Queen sago palm	*Cycas rumphii* Miq.	Near Threatened ver. 3.1	2
Gnetaceae			
	Gnetum latifolium Bl.		2
	Gnetum montanum Markgraf		2
Pterophyta			
Adiantaceae			
Tailed madienhair	*Adiantum caudatum* L.		2
	Adiantum flabellulatum L.		2
	Adiantum semiorbiculatum Bonap.		2
Ox-tounge fern	*Antrophyum callifolium* Bl.		2
Angiopteridaceae			
	Angiopteris annamensis C.Chr. & Tardieu		2
Aspleniaceae			
	Asplenium cheilosorum Kunze ex Mett.		2
	Asplenium coenobiale Hance		2
	Asplenium falcatum Lam.		2
	Asplenium hainanense Ching		2
	Asplenium neolaserpitiifolium Tardieu & Ching		2
	Asplenium pseudolaserpitiifolium Ching		2
Variable speenwort	*Asplenium varians* Wall. ex Hook. & Grev.		2
	Diplazium malaccense C.Presl		2
	Diplazium platychlamys C.Chr.		2
	Diplazium polypodioides Bl.		2
Blechnaceae			
Oriential blechnum	*Blechnum orientale* L.		2
Cyatheaceae			
	Cyathea contaminans (Wall. ex Hook.) Copel.		2
	Cyathea podophylla (Hook.) Copel.		2
Davalliaceae			
Narrow swordfern	*Nephrolepis cordifolia* (L.) Presl		2
Scaly swordfern	*Nephrolepis hirsutula* (G Forst.) C.		2

	Presl.		
	Rumohra grossa Tardieu & C.Chr.		2
Dennstaedtiaceae			
	Lindsaea lobata Poir.		2
	Microlepia calvescens (Wall. ex Hook.) Presl.		2
	Microlepia herbacea Ching & C. Chr. ex C. Chr. & Tardieu		2
Common lace fern	*Sphenomeris chinensis* L.		2
Dryopteridaceae			
	Arachniodes henryi (H. Christ) Ching		2
	Tectaria polymorpha (Wall. ex Hook.) Copel.		2
	Tectaria stenosemioides (Alderw.) C. Chr.		2
	Tectaria trichotoma (Fée) Tagawa		2
	Tectaria variabilis Tardieu & Ching		2
	Tectaria vasta (Bl.) Copel.		2
Gleicheniaceae			
Old World forked fern	*Dicranopteris linearis* (Burm.f.) Underwood		2
	Gleichenia truncata (Willd.) Spreng.		2
Hymenophyllaceae			
	Hymenophyllum fimbriatum J. Sm.		2
Isoetaceae			
	Isoetes coromandelina L.f.	Least Concern ver 3.1	2
Lomariopsidaceae			
	Bolbitis cadieri (Christ) Ching		2
	Bolbitis subcordata (Copel.) Ching		2
Marsileaceae			
Four leaf clover	*Marsilea quadrifolia* L.		2
Ophioglossaceae			
Stalked adder's tounge fern	*Ophioglossum petiolatum* Hooker		2
Polypodiaceae			
	Colysis digitata (Bak.) Ching.		2
	Colysis wrightii (Hook.) Ching.		2
	Colysis wui (C. Chr.) Ching		2
	Drynaria fortunei (Kunze) J. Sm.		2
Java fern	*Microsorum pteropus* Bl.		2
	Phymatosorus longissimus (Bl.) Pic. Serm.		2
Regal elkhorn fern	*Platycerium grande* (A.Cunn) J.Sm.		2
	Pyrrosia adnescens (G. Forst.) Ching		2
	Pyrrosia eberhardtii (Christ) Ching		2
Pteridaceae			

Silver lace fern	*Pteris ensiformis* Burm. F		2
	Pteris grevilleana Wall. ex J. Agardh		2
Psilotaceae			
Flatfork fern	*Psilotum complanatum* Sw.		2
Whisk fern	*Psilotum nudum* L. P. Beauv.		2
Schizaeaceae			
Climbing fern	*Lygodium conforme* C. Chr.		2
	Lygodium flexuosum (L.) Sw.		2
Japanese climbing fern	*Lygodium japonicum* (Thunb. ex Murr.) Sw		2
Selaginellaceae			
	Selaginella boninensis Bak.		2
	Selaginella petelotii Alston		2
	Selaginella trachyphylla A. Braun ex Hieron		2
Thelypteridaceae			
	Cyclosorus philippinarum (Fée) Copel.		2
	Pronephrium simplex (Hook.) Holtt.		2
	Sphaerostephanos heterocarpus (Bl.) Holtt.		2
	Thelypteris triphylla (Sw.) K. Iwats.		2