

**The socio-ecology of the black-shanked douc  
(*Pygathrix nigripes*)  
in Mondulhiri Province, Cambodia**



Photo by Allan Michaud

**by  
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A thesis submitted for the degree of Doctor of Philosophy  
of The Australian National University in Biological Anthropology  
School of Archaeology and Anthropology

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### **Statement of originality**

The work presented in this thesis is, to the best of my knowledge and belief, original and my own work, except where acknowledged. Material has not been submitted either in whole or in part, for a degree at this or any other university.

A handwritten signature in black ink, appearing to read 'Benjamin Miles Rawson', with a long horizontal flourish extending to the right.

**Benjamin Miles Rawson**



Dedicated to Michelle, Anne and Howard  
for your faith in me and the sacrifices you have made





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# **Abstract**

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This thesis details research into the ecology and behaviour of the black-shanked douc (*Pygathrix nigripes* Milne-Edwards, 1871), an Endangered colobine found in eastern Cambodia and southern Vietnam. The study was conducted in Seima Biodiversity Conservation Area (SBCA), Mondulhiri Province, Cambodia, over a period of 20 months, from January 2003 to August 2004, and therefore represents the longest-term study of any species in the genus.

Distributional and relative density data show that black-shanked doucs preferentially utilise evergreen forest. There they maintain the largest group sizes and highest relative densities. The species is also commonly found in semi-evergreen and mixed deciduous forest, although the latter may be sub-optimal due to limited food resources. *P. nigripes* additionally occurs in dry deciduous dipterocarp forest but probably only where it is associated with one of the first three forest types. Group sizes appear to be lower in sub-optimal habitats as suggested by the ecological constraints model.

Four major social units occur in the species: one-male units (OMUs), bands comprised of several OMUs, bachelor groups and lone males. OMUs averaged 7.5 individuals, and were composed of a single male, several females and offspring. Black-shanked doucs have a fission-fusion social system, with fusion of OMUs into bands occurring more commonly in the wet season. The maximum band size recorded was 26 individuals.

Activity budgets were similar to other colobine species. Inactivity dominated with a frequency of 61%, feeding 27%, travel 6%, social behaviour 3%, and other activities 2%. Daily distribution of activities was also a typically colobine pattern with high rates of feeding in the morning, a long midday period of inactivity followed by a second feeding bout in the afternoon. Locomotion was predominantly quadrupedal although frequencies of brachiation were significant. The majority of activities occurred in the middle to upper forest canopy: only one instance of terrestriality was recorded. Several behaviours not previously documented in wild doucs were observed, including paternalistic behaviour and allomothering.

Contrary to previous studies on the feeding ecology of *Pygathrix*, *P. nigripes* at the site was best characterised as a seed predator, with 40% of feeding records being dedicated to seeds. Leaves, especially young leaves, also comprised a significant part of the diet.

Doucs were highly selective in their diet, feeding from only 35 positively-identified plant species and with 44% of all feeding records coming from only five species. Legume species were heavily targeted. Diets did not track resource abundance across seasons with the exception of high levels of flower consumption correlated with high availability during the dry season and seed consumption during the wet season.

SBCA holds the largest known population of the species across its range and is under active conservation management by the Wildlife Conservation Society and the Forestry Administration of the Royal Government of Cambodia and therefore represents one of the best opportunities for long-term conservation of the species. Having an understanding of habitat preferences, feeding ecology and behaviour as presented in this thesis provides a basis for management of the species at this site and beyond.

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## ***Introduction***

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### **Thesis overview**

#### ***Background to the current research***

Socio-ecological studies on the genus *Pygathrix* have, until relatively recently, been virtually non-existent, to the point that the genus has been called “...the most unstudied primates in the Old World”(Bennett and Davies, 1994). This lack of research is largely a consequence of the recent history of civil strife and warfare in the region where they occur, most notably a consequence of the American-Vietnam war and the Khmer Rouge’s rise to power. In the past decade however a strongly emerging primatological tradition has been developing in Vietnam, Cambodia and Lao PDR, and research into the region’s primate fauna is going on apace, driven largely by in-country nationals.

In 2002, when this research was conceived, very little was known about the black-shanked douc (*P. nigripes*). Distributional data were very poor with, for example, only a handful of locality records for Cambodia (Kirkpatrick, 1998b, Long, 2000, Long *et al.*, 2000), which is now known to be the species’ major stronghold (Pollard *et al.*, 2007). Very little socio-ecological information was available, and the best one could do was to assume that it would be similar to that of the more northerly distributed and better studied red-shanked douc (*P. nemaeus*) (Lippold, 1977, Lippold, 1998). No data were available on population abundance, and as such assessing the species status was problematic.

Since that time our understanding of these issues has grown. Research has been conducted into the species’ socio-ecology (Rawson, 2006, Hoang Minh Duc and Baxter, 2006b, Hoang Minh Duc, 2007), distribution and population status (Ha Thang Long, 2002, Phan Duy Thuc *et al.*, 2005, Hoang Minh Duc and Baxter, 2006a, Pollard *et al.*, 2007, Hoang Minh Duc, 2007, Rawson and Roos, 2008). Based on this emerging understanding of the species, its conservation status was reassessed in September 2006 during the IUCN’s Asian Primate Red List Workshop, held in Phnom Penh, Cambodia. The black-shanked douc is currently listed on the IUCN Red List as “Endangered A2cd”, based on a  $\geq 50\%$  reduction in population size over the last three generations, driven by hunting pressure across a large proportion of their range and conversion of lowland forest to agriculture (Rawson *et al.*, 2008).

The vast majority of this recent research into the genus *Pygathrix* generally, and black-shanked doucs specifically, has been conducted in Vietnam (Phan Duy Thuc *et al.*, 2005, Hoang Minh Duc, 2007, O'Brien *et al.*, 2008). Research in Cambodia, the other country in which the species is distributed and where this current study was conducted, has revolved around Seima Biodiversity Conservation Area (SBCA), Mondulhiri Province. Study of the population of *P. nigripes* in SBCA is vital for gaining a clear understanding of the species' socio-ecology, probably more so than anywhere else throughout its distribution. This is because the population here occurs at what appears to be natural densities with little or no hunting pressure and natural, as opposed to anthropogenic, population fragmentation driven by the diversity of forest types at the site (Zimmermann and Clements, 2002, Pollard *et al.*, 2007, Clements *et al.*, 2008, Rawson *et al.*, 2008). Conversely, most, if not all, sites in Vietnam where the species is found have suffered massive population declines due to hunting pressure and forest conversion and exploitation, with populations fragmented and, in most locations, remnant (Nadler *et al.*, 2003, Nadler *et al.*, 2007, Rawson *et al.*, 2008). As such, disentangling elements of the species' natural history from anthropogenic influences can be problematic in these areas.

The current study therefore provides a vital window through which to view the black-shanked douc, its social interactions, and those with its environment. An understanding of the species' socio-ecology is important not only for what it teaches us about patterns of behaviour and ecology in primates, but even more importantly, how it educates us about the best approaches to conserve the species into the future.

## ***Research aim***

This thesis aims to elucidate various aspects of *P. nigripes* socio-ecology. Specifically it asks, "How is the socio-ecology of *Pygathrix nigripes* best characterised and how do environmental and temporal factors affect the species' activity budgets, group dynamics and feeding ecology?" Under this general question, a number of research questions were addressed during this study. Broad avenues directing research and the specific questions associated with them are detailed below.

1. What is the activity budget of *P. nigripes*?
  - a. Does *P. nigripes* fit the colobine paradigm in how time is partitioned between various activities?

- b. How do activity budgets vary temporally over seasons and through the day?
  - c. What are the dominant forms of locomotion in *P. nigripes*?
  - d. How is sociality expressed in *P. nigripes*?
2. What are the key social groupings found in *P. nigripes*?
- a. Do doucs form one-male multi-female units or multi-male multi-female units?
  - b. Do doucs have a fission-fusion social system?
  - c. Do temporal and spatial trends in resource availability affect social groupings?
3. What habitats do *P. nigripes* utilise?
- a. What are appropriate and inappropriate habitats in SBCA for supporting populations of *P. nigripes*?
  - b. How is density and distribution of *P. nigripes* affected by habitats within the forest mosaic of SBCA?
4. What is the feeding ecology of *P. nigripes*?
- a. Are black-shanked doucs selective feeders or generalists?
  - b. Is *P. nigripes* better categorised as a leaf eater or a seed predator?
  - c. What plant species provide the bulk of the diet for *P. nigripes* in SBCA and are there any critical keystone species?
  - d. Does diet change seasonally and if so why?
  - e. What are the implications of *P. nigripes*' food selectivity on their distribution in SBCA?
  - f. What are the potential impacts on *P. nigripes* of selective logging in SBCA?

### ***Research significance***

The genus *Pygathrix* has been one of the least studied of the Old World primates (Bennett and Davies, 1994), with information about the black-shanked douc' s socio-ecology being totally lacking until the current research was begun. This thesis details important factors of *Pygathrix* socio-ecology, including social structure and grouping patterns, activity budgets, feeding ecology and habitat use and preferences. These

aspects of socio-ecology are discussed in a context of behavioural and ecological theory, and as such add to our understanding of models dominant in the literature. Additionally, the current study puts black-shanked doucs into context in relation to other odd-nosed colobines and the subfamily Colobinae more generally, increasing our understanding of these rare and threatened species.

This thesis also has several implications in terms of the conservation of *P. nigripes*. The SBCA constitutes the largest global stronghold for *P. nigripes*, with a population in the vicinity of 42,000 individuals (Pollard *et al.*, 2007), dwarfing all other known populations of this Endangered primate by two orders of magnitude. As such, detailed ecological knowledge about the species at this site is vital to ensure effective long-term management of this population. This thesis provides the groundwork for understanding the driving factors influencing the species' distribution and abundance at the site. It also provides suggestions as to the possible impacts that anthropogenic activities at the site may have on the species, specifically how commercial removal of key plant species from the habitat may impact on the site's ability to maintain the population. This thesis therefore represents a vital piece of the puzzle required for effective management of the species in SBCA to ensure long-term conservation of the species at the site and beyond.

### ***Research limitations***

While the current research provides insight into the species' socio-ecology, there were several limitations which impacted on the scope of the study. The most important of these was the fact that study animals were never habituated to human presence. This, along with poor viewing conditions in dense semi-evergreen forest, and my own recurring bouts of malaria, made datasets patchy in places, reducing the ability of statistical tests to detect trends in data. It also precluded individual recognition of studied animals and, as such, key questions concerning ranging behaviour in the species were not adequately addressed. Due to financial restrictions and lack of in-country facilities and expertise, no chemical analyses of plant parts fed on by doucs were performed, and identifications of plant species throughout the study were piecemeal in approach.

### ***Thesis outline***

Chapter one provides an overview of the research aims and limitations presented within this thesis. It also provides a broad overview of the current state of knowledge

concerning genus *Pygathrix* in general and *P. nigripes* specifically as it relates to taxonomy, anatomy, distribution and status. Discussion of *Pygathrix* behaviour and ecology is not presented here as it is covered extensively in other chapters.

Chapter two details the history and biodiversity values of the broader site of SBCA and discusses the particular part of the study site where the majority of data on *P. nigripes* in this thesis comes from. Details on weather, including temperature and rainfall during the study, are also presented.

Chapter three details the methods used during this study. This includes details about how phenology transects were set up and monitored and how behavioural observations were conducted, including the ethogram used during the study. More detailed methods specific to individual chapters are found within each of those chapters.

Chapter four details the vegetation of the study site. This includes data on forest structure, vegetation richness and diversity, and seasonal patterns in phenologies of flower, fruit and leaf, based on phenology transect monitoring. The forest is characterised with dominant and sub-dominant species identified and seasonal resource abundance documented. A clarification of habitat typologies in relation to these data is also presented for later clarification about impacts of forest type on *P. nigripes*' socio-ecology.

Chapter five describes the activity budget of *P. nigripes*, providing insight into how black-shanked doucs allocate time to different activity classes such as travelling, feeding, locomoting, and in social pursuits. Daily and seasonal temporal variation in activity budgets are described as are differences between age and sex classes. Detailed descriptions of some social behaviours such as allomothering and copulation are also provided.

Chapter six details group size and group composition in *P. nigripes*. The basic social groupings of the species are identified, and a discussion of group fission-fusion in the genus presented. Correlates of group size and composition are discussed within the context of socio-ecological models, including the effect of habitat type and seasonality.

Chapter seven describes the feeding ecology of *P. nigripes*. Key plant species in their diet are determined and selection ratios based on the relative abundance of plant species presented to provide insights into key resources utilised by the doucs. The feeding

strategy of *P. nigripes* is presented and the implications for conservation and distribution of the species in relation to habitat and plant species' distributions are discussed.

Chapter eight presents a brief summary of the key findings and conclusions of the thesis.

## **Putting *Pygathrix nigripes* into context**

### ***Taxonomy and anatomy***

#### **Overview above the generic level**

Doucs have generally been placed in the family Cercopithecidae and the subfamily Colobinae. The Colobinae and Cercopithecinae are readily distinguished based on various morphological traits, one of the most striking being the former's multi-chambered, or complex, stomach containing symbiotic organisms. These are used for breaking down and digesting cellulose (Chivers, 1994, Caton, 1998), a component of leaves, which has led to the moniker for the subfamily, the "leaf-eating monkeys". This adaptation has arguably had a large effect on many aspects of colobine ecology and behaviour (Kirkpatrick, 1998a, 1999, Kirkpatrick, 2007). Other gross morphologies associated with the high levels of folivory found amongst the Colobinae include large salivary glands (Groves, 1989), and large high cusped teeth structured to process leaves and seeds (Lucas and Teaford, 1994) and the absence of cheek-pouches (Caton, 1991). Other cranial and post-cranial morphological differences between the two subfamilies is the Colobinae's wider inter-orbital region, deeper mandibles, reduced or absent thumbs, long tails, and hindlimbs longer than forelimbs (i.e. a low intermembral index) (Fleagle, 1999) (see Groves, 1989, 2000 for a comprehensive review).

The subdivision of the Colobinae is slightly more controversial, with argument centring over the monophyly of the African and Asian types. Morphologically the two clades are not easily distinguished. African species have several derived features: a vestigial thumb, reduced to the point that the pollex is absent or only very small (Oates *et al.*, 1994, Groves, 2001); dentally their  $M_3$  is posteriorly broader than anteriorly and the protoconid of  $P_3$  is reduced (Groves, 1989); and they show various pedal specialisations (Groves, 2001). Asian colobines' cranial morphology shows the presence of a suborbital fossa and a shorter face than that of the African species (Oates *et al.*, 1994).

Genetic and karyological evidence suggests more convincingly that Asian and African colobines are monophyletic groups (Morales *et al.*, 1999, Zhang and Ryder, 1998b, Bigoni *et al.*, 2004). Page *et al.* (1999), in a study of a subset of colobine taxa, confirmed that *Trachypithecus* and *Nasalis* form a clade as do studied African taxa, suggesting the groups are monophyletic. They split them, based on a time-based taxonomic ranking system (Goodman *et al.*, 1998), as subtribe Presbytina for the Asian forms and subtribe Colobina for the African forms, as per Delson (1994), saying that they diverged approximately 10-9 Ma.

### **Overview at the generic level**

The taxonomy of the doucs at the generic level and below has been in some dispute since it was first described, and especially so in recent times. Disagreement has focused on two main issues: firstly, what is the douc's taxonomic affinity to the snub-nosed monkeys, the proboscis monkey, and the fossil taxon *Mesopithecus pentelicus*; and secondly, how many species or subspecies of douc should be recognised (Jablonski, 1995)?

### **Affinities with *Rhinopithecus***

Few primatologists have doubted the closeness of the snub-nosed monkeys to the doucs, but there have been changing opinions as to how these taxa should be ranked relative to each other (Jablonski, 1995). The snub-nosed monkeys were recognised as a genus in their own right until Groves (1970) placed them under the genus *Pygathrix*, as subgenus *Rhinopithecus*, based on the cranial differences and the external morphology of the nose (Groves, 1989, Groves, 2001). This taxonomic ranking was used by most subsequent authors until the 1990s (e.g. Napier, 1985, Davies and Oates, 1994).

This taxonomic arrangement was first questioned after morphological analysis suggested that *Rhinopithecus* and *Pygathrix* should be classified as separate genera, and indeed that *Rhinopithecus* contained two subgenera, *Presbytiscus* for the Tonkin snub-nosed monkeys, and *Rhinopithecus* containing the three Chinese taxa (Jablonski and Peng, 1993, Jablonski, 1995). Further work, which included the additional taxa *Nasalis* and the fossil *Mesopithecus*, suggested that *Rhinopithecus* and *Pygathrix* were not even sister taxa, with *Pygathrix* grouping instead with *Nasalis* and *Mesopithecus*, while *P. avunculus* grouped with *Rhinopithecus* (Jablonski, 1998, contrary to Peng *et al.*, 1993). This finding, that *Pygathrix* and *Rhinopithecus* do not form a monophyletic group, was

and remains a strong argument for elevating the snub-nosed monkeys from their subgeneric status under *Pygathrix* to full generic status.

Genetic evidence showed that *Pygathrix* and *Rhinopithecus* (based on *R. bieti* and *R. roxellana*) are monophyletic and the difference between the two genera (15%) is also probably sufficiently large to warrant generic status, and that, at least compared to *Trachypithecus*, the two were sister taxa (Wang *et al.*, 1997, contrary to Wang *et al.*, 1995). The work of Roos (in Nadler *et al.*, 2003) also suggested this to be the case, with *Trachypithecus* branching off first. Further evidence that the two are sister groups came from Zhang and Ryders' (1998a) genetic analysis, which demonstrated the two were closer to each other than either was to *Semnopithecus entellus*, although their assertion that *Rhinopithecus* should be distinguished at the generic level, based on a diversion time of two million years, does not stand up to the Goodman *et al* (1998) time-based classificatory system. They (Zhang and Ryder, 1998b) restated *Rhinopithecus*' generic status in other work and with the inclusion of *Nasalis* found *Rhinopithecus* to group closer to it than it did to *Pygathrix*.

The two key issues here are: firstly, whether *Rhinopithecus* is considered a full genus or a subgenus under *Pygathrix*; and secondly, whether *Pygathrix* and *Rhinopithecus* are sister taxa. On the first count there is sufficient evidence to consider the Chinese and Vietnamese odd-nosed monkeys as a monophyletic group and as a separate genus, a move which is now commonly accepted (Groves, 2001, Groves, 2004a, Brandon-Jones *et al.*, 2004). On the second count it seems that, although *Pygathrix* may be closer to *Rhinopithecus* than *Semnopithecus* and *Trachypithecus*, there is yet insufficient information to say categorically that they are sister groups.

### **Affinities with *Nasalis***

While *Pygathrix*'s affinity with *Rhinopithecus* had long been under debate, Jablonski (1998) was the first to suggest a close taxonomic affinity between *Pygathrix* and both *Nasalis larvatus* and *Mesopithecus pentelicus* (a finding later supported by Groves, 2000). Based on her cladistic analyses of these and other taxa, she created a *P. nemaus* – *M. pentelicus* – *N. larvatus* clade as a sister group to *Rhinopithecus*. This was an unexpected assertion on several levels.

Firstly, a close affiliation with *N. larvatus* seemed unlikely due to large morphological differences. The proboscis monkeys' distinctive cranial morphology has often placed it

at the opposite end of Colobinae taxonomy to *Pygathrix* (Groves, 1970, Groves, 1989), with *Nasalis* described as primitive (Groves, 2000). *Nasalis* also has uniquely shaped enamel prisms on its teeth (Dostal and Zapfe, 1986), and the pelage of the *N. larvatus* neonate does not markedly contrast with that of the adult (Groves, 1989) as is found in the other Asian colobines, although the neonate does share the distinctive blue facial skin of the other odd-nosed colobines (Chaplin and Jablonski, 1998). Characters that *N. larvatus* shares with *Rhinopithecus* but not with *Pygathrix*, such as large body size and terrestrial habits (Napier and Napier, 1985), have been interpreted as symplesiomorphic characters (Peng *et al.*, 1993).

Secondly, and possibly more problematic than these phenetic issues, is the fact that *Pygathrix* shares the same diploid number of chromosomes ( $2n = 44$ ) (Bigoni *et al.*, 2004) as all studied colobines of both African and Asian origins (Giusto and Margulis, 1981), with the one exception being *Nasalis larvatus* which has a diploid number of  $2n = 48$  (Bigoni *et al.*, 2003). This fact has generally resulted in *N. larvatus* being considered primitive to, and somewhat different from, other Asian colobids, to the extent that at times it has been given its own subfamily Nasalinae (grouped with *Nasalis concolor*, now *Simias concolor* (Groves, 1989, Groves, 2001), although it is now generally accepted to be firmly within the Asian colobine clade (e.g. Collura *et al.*, 1996, Page *et al.*, 1999, Groves, 2001, Brandon-Jones *et al.*, 2004).

More recent work however suggests that karyologically *Pygathrix* might be closer to *N. larvatus* than previously expected, with *Nasalis* actually showing a derived karyotype (Bigoni *et al.*, 2003) from the more conservative *Pygathrix* arrangement (Bigoni *et al.*, 2004). In this scheme *Nasalis* is the first to diverge, after which two chromosomal fissions occur, giving it its unique chromosomal count, a suggestion supported by karyotypic fission theory (Giusto and Margulis, 1981). Roos' (personal communication) genetic work has found that while *Nasalis-Rhinopithecus-Pygathrix* form a strongly supported clade, relationships between them remain unsolved, with *Pygathrix* grouping with *Nasalis* in some trees and with *Rhinopithecus* in others. Therefore, while the genetic evidence presented here is phylogenetically instructive for the odd-nosed colobines overall, there is still insufficient genetic evidence to suggest that *Pygathrix* is closer to *N. larvatus* than it is to *Rhinopithecus* as suggested by Jablonski (1998).

In contrast to these factors that apparently set *Nasalis* and *Pygathrix* apart, there are traits which are common between the two which possibly suggest a close phylogenetic origin. Firstly, both share a white sacral patch and white tails (Napier and Napier, 1985), which has been pointed out as “one of the most distinctive features uniting any of the odd-nosed colobines” and may facilitate animals to follow each other along arboreal pathways (Chaplin and Jablonski, 1998, p95). It has also been noted that they share a high inter-membral index (Groves, 1989), 93-94 for *Pygathrix* (Napier and Napier, 1985, Workman and Covert, 2005) and 93 for *N. larvatus* (Napier and Napier, 1985), in contrast to the much lower indices found in other Asian colobines, except perhaps *Rhinopithecus avunculus* (Herbert Covert, pers. comm.). Higher intermembral indices generally suggest that a species utilises more suspensory postures (Fleagle, 1999), an issue followed up in Chapter 5. Further, hybridisation between the species is possible, as evidenced by a successful mating at Zoo Erfurt, Germany; the individual died before it was determined whether it was fertile (Benirschke *et al.*, 2004).

Another approach that has been pursued to elucidate the relationships amongst the odd-nosed colobines has been studies of digestive physiology. Gut histology and gross anatomy of course relate to diet, and the colobines are unique amongst primates in having a complex stomach with associated symbiotic bacteria which allows breakdown of cellulose (Caton, 1999). Within the Colobinae further divisions, based on gut morphology, can be made, e.g. quadripartite or tripartite stomachs, small intestine length etc. (Caton, 1999). Caton’s (1998) analysis of the gastro-intestinal tract of *Pygathrix nigripes*, *Nasalis larvatus* and *Rhinopithecus* spp. suggested that the most parsimonious phylogenetic relationship grouped *P. nemausus* with *N. larvatus*, while *Rhinopithecus* grouped most closely with *Procolobus*. The study was problematic on several counts, however. Firstly, only eleven character states were used; secondly, only one *Pygathrix* specimen was available, an infant which would not have developed histologically (Caton, 1998); and thirdly, other studies (Chivers, 1994, Edwards and Killmar, 2004) showed relative gut dimensions between the two at least to be quite different, with a larger number of species studied. Additionally, a grouping of *Rhinopithecus* with the African *Procolobus* seems highly unlikely, casting doubt on the explanatory power of the comparisons used.

In short, it currently seems that *Pygathrix*'s affinity with *Nasalis* can not be determined with any level of certainty. In all likelihood, it will require more work done at the chromosomal and genetic level to elucidate this relationship.

### **Affinities with *Mesopithecus***

An additional reason that Jablonski's (1998) analysis was surprising was because the fossil taxon *Mesopithecus* had usually either been seen to be more closely related to African than Asian colobines (Strasser & Delson 1987) or, when considered to be affiliated to the latter, was seen as a *Semnopithecus*-like form, based on its anatomically apparent terrestrial behaviour and palaeoenvironmental reconstructions (Delson, 1994, Fleagle, 1999). However, work based on dental enamel prisms (Dostal and Zapfe, 1986), hard tissue evidence (Byron, 2001), and more recently on dental metrics (Pan *et al.*, 2004), clearly shows that *Mesopithecus* should be grouped with the Asian colobines, and further suggests it be included with the odd-nosed colobines (possibly including *Nasalis*) in a newly erected tribe, the Rhinopithicini (Groves, 2000, Pan *et al.*, 2004). As an Asian colobine and ancestor of *Pygathrix*, *Mesopithecus* may have dispersed east into broadleaf evergreen and deciduous forested areas in eastern Asia, and then dispersed southwards into south-east Asia (Pan *et al.*, 2004). By this account, the tropical adaptations of *Pygathrix* and especially *Nasalis* would be derived not primitive, although whether *Mesopithecus* is most closely related to *Pygathrix* or *N. larvatus* is a matter still open for debate.

### **Speciation in the genus *Pygathrix***

The red-shanked douc, described by Buffon in 1765 as "The Douc or Cochin-China Monkey", was the first species of the genus described. Linnaeus (1771) later awarded it the name *Simia nemeus*, and in 1812 E. Geoffrey St. Hilaire placed it in a new genus *Pygathrix*, giving it its presently accepted binomial. In 1871 Milne-Edwards described a second species, *Semnopithecus nigripes*, for the black-shanked form, based on a specimen from Saigon, Vietnam. This was followed by Kloss' (1926) description of a third form from Lang Bian, Vietnam, claimed to be intermediate between the two, *Presbytis nemeus moi*. Ellerman and Morrison-Scott (1951) downgraded the black-shanked form to a subspecies under *Pygathrix nemeus* and synonymised *Pygathrix moi* with it; this latter step has generally been accepted by all subsequent authors (although see Brandon-Jones *et al.*, 2004) and has recently been confirmed with molecular data (Roos, 2004).

In the 1990s came the suggestion there may be an additional undescribed species of douc. Wirth *et al.* (1991) published photographs of a subadult female of unknown provenance being kept in captivity in Ho Chi Minh City, which clearly displayed pelage different to that of either *Pygathrix nemaus* or *P. nigripes*, most notably lacking the white “sleeves” and red legs of the former and the blue muzzle and spectacled appearance of the latter. Description of a second animal (Lippold and Vu Ngoc Thanh, 1995), confiscated in the Central Highlands of Vietnam, showed similar characteristics, adding further weight to the suspicion that an undescribed species was present in this area.

With the establishment of the Endangered Primate Rescue Centre (EPRC) at Cuc Phuong in 1993 (Nadler, 1996) came the opportunity to house confiscated animals in an environment conducive to observation and research. It soon became apparent with the confiscation of five doucs similar to that described by Wirth *et al.* (1991) that we were indeed in the presence of an unknown taxon. Subsequently Nadler (1997) described it as a new subspecies, *Pygathrix nemaus cinereus*, a designation which was later changed to *P. n. cinerea* to bring it into accord with the feminine gender of the generic name (Brandon-Jones *et al.*, 2004).

Later craniometric analysis by Harding and Groves (2001) showed consistent differences in size and demonstrated that the three taxa grouped separately based on other cranial characters (J. Harding, pers. comm.). They therefore suggested full species status, given that cranial differences between *P. cinerea* and the other douc taxa are similar to those between *P. nemaus* and *P. nigripes*. Genetic evidence also largely supports this division. Distances between *P. cinerea* and *P. nemaus*, based on the mitochondrial cytochrome b gene, averaged 2.69% (Roos and Nadler, 2001) and in a further test 2.8 – 3.4% (Roos, 2004), and most subsequent authors have also recognised the taxon at the specific rather than subspecific level (Groves, 2001, Groves, 2004a), except for Brandon-Jones *et al.* (2004) who provisionally ranked it as a subspecies of *P. nemaus*. These latter authors went on to suggest that, based on *P. cinereas*' geographic distribution, *Presbytis nemaus moi* may be a senior synonym for the taxon, but Groves (2004b) found that inspection of the type specimen of *Presbytis nemaus moi* clearly shows it represents a junior synonym of *Pygathrix nigripes* and not a representative of *Pygathrix cinerea*.

Taking a back seat to this excitement was the taxonomy of the black-shanked douc which had remained a subspecies of *Pygathrix nemaeus* since its relegation in 1951 (Ellerman and Morrison-Scott). Brandon-Jones (1984) proposed to reinstate it to species status based on the fact that it was cranially diagnosable, but this was not followed by the majority of authors until 2001 when a sea change of opinion elevated it back to a full species. This was based on the molecular evidence of Roos (2001), and later supported further (Roos, 2004), which showed a large average difference (7.69%) from the *P. nemaeus*-*P. cinerea* clade.

So currently three monophyletic species are generally recognised: the red-shanked form *Pygathrix nemaeus*, the black-shanked form *Pygathrix nigripes*, and the grey-shanked form *Pygathrix cinerea*. Little work has been done on the phylogenetic relationships between the three taxa, being limited to molecular studies on the mitochondrial cytochrome b gene. This work, however, based on molecular distances, suggests that *Pygathrix nigripes* diverged first and forms a sister group to the *P. nemaeus*-*P. cinerea* clade, who diverged from each other at a later stage (Roos and Nadler, 2001, Roos, 2004). Interestingly, Roos and Nadler's (2001) data suggested that within both *P. nemaeus* and *P. nigripes* there were two clades, possibly representing geographic variation or subspecies differentiation. Clarification of this possibility will have to await further work.

## ***Distribution and status***

### **Distribution of genus *Pygathrix***

Although no fossil evidence of *Pygathrix* exists (Nisbett and Ciochon, 1993), it appears that their current distribution, restricted to the east of the lower Mekong River, probably reflects their prehistoric distribution. The Mekong River appears to be an important biogeographical barrier for some Indochinese primate species (Fooden, 1996), as well as some other non-volant mammal taxa (Meijaard and Groves, 2006). It dictates the western edge of the distribution of *Nomascus*, *Pygathrix*, *Rhinopithecus*, the limestone langurs (i.e. some of the *Trachypithecus* species) and *Nycticebus pygmaeus*, all of which are rainforest taxa (Fooden, 1996, Groves, 2004b, Meijaard and Groves, 2006, Groves, 2007). Some taxa however are unaffected, such as the silvered langurs, *Macaca* and *Nycticebus bengalensis*, occurring on both sides of the Mekong River (Fooden, 1996, Meijaard and Groves, 2006).

It is hypothesised that, in the Late Pliocene-Early Pleistocene, environmental changes leading to alternations in forest cover may have restricted many mammal fauna to the Annamite mountains (Meijaard and Groves, 2006). During glacial events the Annamite mountains would have retained tropical forest, and as such this region would have acted as a refugium for forest species, including doucs. After the Pleistocene ended, tropical forests and adapted species, began to spread back into the lowlands. However, the Mekong River, which previously had flowed some 600 km west of its current course, had moved to its current position (Meijaard and Groves, 2006). Therefore, westerly dispersal of mammal species ill-adapted for swimming was restricted by its new course. The presence of primates on both east and west sides of the Mekong is suggested to be a consequence of relatively recent radical meandering changes in the course of the Mekong, which allowed passive dispersal to its eastern bank (Meijaard and Groves, 2006). These species are not rainforest specialists, and were therefore not previously restricted to rainforest refugia (Meijaard and Groves, 2006).

Fooden (1996) noted that a second general theme in the distribution of Indochinese primates east of the Mekong River was also present: a latitudinal divide was apparent for many species groups, with species replacement or distributional limits at around 14-17° N. This is true for all primate taxa, except stump-tailed macaques (*Macaca arctoides*) and the slow loris (*Nycticebus bengalensis*) whose distributions cross this divide (Fooden, 1996, Groves, 2007), and many non-primate taxa as well (Fooden, 1996). This transition zone reflects the change between the southerly tropical climes and the more seasonal northerly ones (Fooden, 1996, Groves, 2007).

This basic pattern of distribution appears to be broadly applicable to the genus *Pygathrix*, which shows species replacement in a general south-north transition (see Nadler *et al.*, 2003 for a detailed description of douc distribution). *Pygathrix nigripes* is the southern-most species, *P. nemaus* the most northerly distributed, with *P. cinerea* intermediate and overlapping the distributions of the other two (Nadler *et al.*, 2003). Groves (2007) has suggested, in fact, that *P. cinerea* may be a taxon of hybrid origin between *P. nigripes* and *P. nemaus* that has been successful in spreading from its point of origin. All three species of douc are found in Vietnam (Nadler *et al.*, 2003), only one, *P. nemaus*, is currently known from Laos PDR (Timmins and Duckworth, 1999), and both *P. nigripes* and, as has been more recently discovered, *P. nemaus*, are known from Cambodia (Rawson and Roos, 2008).

The current state of knowledge of the distribution of doucs in Vietnam has been quite exhaustively reviewed in recent years (Kirkpatrick, 1998b, Nadler *et al.*, 2003, Ha Thang Long, 2004, Ha Thang Long, 2007). This should not be taken to mean that current and historical distributions are well known here. This is far from the case, and sympatry, parapatry and hybridity of the three douc species are still little understood. Distributions in Laos are even less well understood than in Vietnam, surveys in the country only beginning in earnest in 1992 (Ruggeri and Timmins, 1995-1996). Distribution data for Cambodia were very poor a decade ago, with, for example, a gazetteer for the genus only having one record for the entire country (Kirkpatrick, 1998b). In recent years this has improved, with presence/absence data from many of the country's protected areas now available, although distribution within these areas, and outside of the protected area network, is still generally lacking.

### **Distribution of *Pygathrix nigripes***

*Pygathrix nigripes* represents the southernmost species in the genus' north-south distribution, and is found at its most southerly extent in Ta Kou Nature Reserve at around 10°41'N (Hoang Minh Duc *et al.*, 2008). The species found here is clearly the black-shanked form as evidenced by photos from the area (Hoang Minh Duc *et al.*, 2008). Historical and provisional records give a similar southerly distributional limit, reaching just south of 11°N in Dong Nai Province where two specimens were collected by C. B. Kloss in 1918, although doucs are now thought to be locally extinct here (Nadler *et al.*, 2003).

The most northerly extension of the black-shanked douc in Vietnam is equivocal, as there is little information as to if, how and where the species intergrades with *Pygathrix cinerea* and *P. nemaeus*. The least equivocal records for current distribution in Vietnam come from Dak Lac Province where sightings and specimens confirm species designation, giving a northerly location of just south of 13°N. Historical and current distributions are most likely further north from here, however. Lippold (1995) gives the northern limit as 14°22'N in Gia Lai Province based on her surveys in the area, but Nadler *et al.* (2003) doubt her species identifications.

Specimens collected from Kon Tum Province in the 1980s are apparently of *Pygathrix nigripes*, but some specimens and observations of live animals from the same localities display intermediate characters (Nadler *et al.*, 2003) and it is unclear how thoroughly and by whom the mentioned museum specimens were examined. The species has been

confirmed from further north in Cambodia, with a record from Voensei district, Ratanakiri Province at N14°00'30.8", E106°45'29.3", where the species is apparently sympatric with *P. nemaesus* (Rawson and Roos, 2008). In terms of east-west distribution, confirmed records come from Vietnamese coastal areas (Nadler, 2008) and extend westwards, theoretically to the Mekong in Cambodia; the most westerly records of which I am aware are still some 50 kms east of the river.

### **Status of *Pygathrix nigripes***

*Pygathrix nigripes* is listed on the IUCN Red List as Endangered A2cd (Rawson *et al.*, 2008), meaning it has suffered a population decline of  $\geq 50\%$  over the last three generations (assessed as 35 years), driven by a reduction in area of occurrence and levels of exploitation. The species is listed on CITES Appendix I, and is protected under Vietnamese Law under Appendix 1B of Decree 32/2006/ND-CP, and listed in the Red Data Book of Vietnam as "Endangered". It is (possibly) protected under Cambodia law under the Law on Forestry NS/RKM/0802/016, Article 49, but it is not listed in Prakas 020 PR.MAFF, which lists all protected species in Cambodia, which only lists *Pygathrix nemaesus*. This appears to be a nomenclature issue, as red-shanked doucs were unknown to occur in Cambodia at the time the Prakas was signed (Rawson and Roos, 2008). The species is not known to occur in Lao PDR.

The population status of *P. nigripes* is much better known than it was a decade ago, at which time no quantitative population studies had been conducted, but there is still considerable uncertainty as to the locations of key populations of the species. The most comprehensive population estimates to date come from SBCA where the current research was conducted. Using distance sampling techniques a population of 42,603 individuals (95% confidence interval of 27,309 – 66,460) was estimated to occur in an area of 1131 km<sup>2</sup> (Pollard *et al.*, 2007, Clements *et al.*, 2008). No other population estimates exist for Cambodia, although the species is confirmed to occur in a number of protected areas, including Snoul Wildlife Sanctuary (Walston *et al.*, 2001), Phnom Prich Wildlife Sanctuary (Timmins and Ou Rattanak, 2001), Mondulkiri Protected Forest, and forests in Voensei and Siem Pang districts, which also support a population of *N. nemaesus* (Rawson and Roos, 2008), while only interview data come from Virachey National Park (Conservation International, 2008, but also see Rawson and Roos, 2008).

In Vietnam, population data are not much better, but it is apparent that populations are generally smaller than those in Cambodia due to widespread hunting and habitat

conversion (Rawson *et al.*, 2008). The largest known population in Vietnam is found in Nui Chau National Park, where an estimated 500-700 individuals reside (Hoang Minh Duc and Ly Ngoc Sam, 2005). Other documented populations include an estimated 109 individuals from the Nam Cat Tien sector of Cat Tien National Park (Phan Duy Thuc *et al.*, 2005), although this is almost certainly an underestimate. The species is known to occur in a number of other protected areas (see Nadler *et al.*, 2003 for a comprehensive listing), although populations appear to be fragmented and remnant in many of these. Areas which may still contain significant populations of the species in Vietnam include Bu Gia Map National Park, which is contiguous with SBCA, and Bi Doup-Nui Ba Nature Reserve.

Hunting is currently considered the major threat to this species, especially in Vietnam where it is heavily persecuted (Nadler *et al.*, 2003). Doucs are most often used for consumption of meat or in traditional medicine (Nadler *et al.*, 2003), with bones being boiled up into “Cao” or monkey balm which is generally utilised locally (Le Trong Trai, 2007). Trade is apparently very high in the species in some locations in Vietnam, for example 44 dried individuals and 60 kg of bones were confiscated in only two months in and around Chu Yang Sin National Park (Le Trong Trai, 2007). There also appears to be some market for the pet trade in southern Vietnam (Rawson *et al.*, 2008).

Loss of habitat has been another major driver in reduced populations, as large areas of forest within the species' distribution were damaged or destroyed during the American-Vietnam war, followed by a demographic explosion which witnessed large areas of habitat converted to agriculture (Nadler *et al.*, 2007, Rawson *et al.*, 2008). The development of large economic concessions and mining concessions in Cambodia in the future is probably the largest threat to the species in Cambodia (Rawson, 2008).



## ***Study area***

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### **Historical overview**

Cambodia's recent history has been one of war and internal strife. Events over the last 35 years have intimately shaped the status of the country's forests and wildlife and the ability of researchers to assess their value. This applies to Mondulhiri Province perhaps more than anywhere else in the country. Warfare along the Vietnam border, proliferation of weapons, unexploded ordnance and banditry conspired to make this region off limits to biologists for long periods of time. Only in recent years has this changed, with the first comprehensive modern biological surveys occurring on the Cambodian side of the border in 2000 (Walston *et al.*, 2001).

The American-Vietnam war, which began in 1959 when Ho Chi Minh declared a people's war, and ended in 1973 when American troops withdrew, placed Cambodia in the firing line. The Ho Chi Minh trail, which supplied the People's Army of Vietnam (PAVN) and the National Front for the Liberation of South Vietnam (NLF) offensives, ran through eastern Cambodia including Mondulhiri province. Many Vietnamese bases were also located in eastern Cambodia, which took advantage of Cambodia's neutral status as America was unable to (legally) attack them. This ended in 1969-70 when the American government began secretly bombing these areas inside Cambodian territory and later also involved troop deployments here. There were some 844 aerial sorties in Keo Seima district alone, the location of the present study, between January 1970 and August 1973 (unpublished data from Cambodian Mine Action Centre), while Snoul, some 57kms from the study site, was the site of one of the largest of the ensuing battles, the town receiving two days of aerial bombardment (Wikipedia, 2007a).

The extent of damage to forest at the study site as a result of the American-Vietnam war is unknown. One can only assume that in some areas it was significant, given the number of air attacks in the area and the amount of unexploded ordnance (UXO) which is still being removed from the vicinity. UXO represents a real threat even now, as locals use simple metal detectors to locate buried metal which is removed and sold for scrap metal at approximately 400 riel/kg (US\$0.10/kg). Accidents are not surprising, given that a large proportion of ordnance dropped during the conflict did not explode and is still live. For example, some 30% of cluster bombs dropped on Laos during the

same conflict are thought not to have detonated (Wikipedia, 2007b). Some 1000 people/year are killed by UXO or mines in Cambodia (SCW, 2006). Indeed, the sister of a research assistant working on the project was killed unearthing a cluster bomb during the project.

Against this backdrop the Khmer Rouge took control of the province in 1969-1970 and relocated the population to Koh Nyek District to work on collectivized farms (Evans *et al.*, 2003). This had the effect of almost totally removing any population from the area surrounding the study site, and people began to return only in the late 1980s (Evans *et al.*, 2003). The effect on the forest and wildlife of the removal of the population from the area over this period of time is unknown, but may have reduced the impacts of exploitation. Populations in the province have apparently always been low, as is currently the case, the vast majority of the province having less than 10 people/km<sup>2</sup> (SCW, 2006).

On 18<sup>th</sup> August 1994, Samling International, a Malaysian logging company, entered into a contract with the Royal Government of Cambodia which gave them a 30-year licence to log an area of 467,484 hectares across the provinces of Monduliri, Kratie and Kampong Cham (Thomas, 2000). This was facilitated by the construction of a road in 1998 (Evans *et al.*, 2003) running from Snoul, through Snoul Wildlife Sanctuary, to Sen Monorom. Samling International originally stopped local people from using this road, but the local government intervened (Global Witness, 1999) and the road was in heavy use by the time I was working at the site.

The effects of the granting of the area as a logging concession on forest health and wildlife can be debated. While, unlike many concessionaires in Cambodia Samling International had a strong background in forestry practices, the company was accused of many illegal activities, including: beginning logging before an official cutting permit was issued; cutting undersized trees; purchasing wood from outside the concession including in Snoul Wildlife Sanctuary; and dealing with the Royal Cambodian Armed Forces, specifically buying timber cut by them, amongst others (Global Witness, 1999). Additionally, the increased access the road provided meant that a large amount of immigration and settlement along the road has occurred. Forest is slashed and burned to make way for *chamkar* and settlements (Figure 2-2), which effectively fragments the forest.

Conversely, Samling International went some way to controlling the rampant illegal logging going on in the lawless border area by strictly controlling access to the area. Much of this logging activity was conducted by Vietnamese crossing the border into Coupe 3, one of the richest areas for timber in the concession, and removing timber back across the border. In addition, negotiations with Wildlife Conservation Society (WCS) resulted in a no hunting agreement, meaning that concessionaire staff were not permitted to hunt wildlife, thus removing a major impact on wildlife populations.

Regardless, in 1999 the Royal Government of Cambodia increased royalty rates on timber by threefold to \$54/m<sup>3</sup> (Global Witness, 1999). Samling International stopped operations at this time in protest and never restarted them, and in 2002 they officially pulled out of Mondulhiri completely, leaving the way open for the gazetting of the Seima Biodiversity Conservation Area (SBCA). During the time that Samling was operational, it selectively logged Coupes 1 and 2a of the 15 designated coupes. Despite the fact that a very small area was legally exploited in recent times, many areas have old logging roads which have been used for small scale logging at indeterminate times in the past, either by locals or Vietnamese, and low level disturbance is evident in many areas.

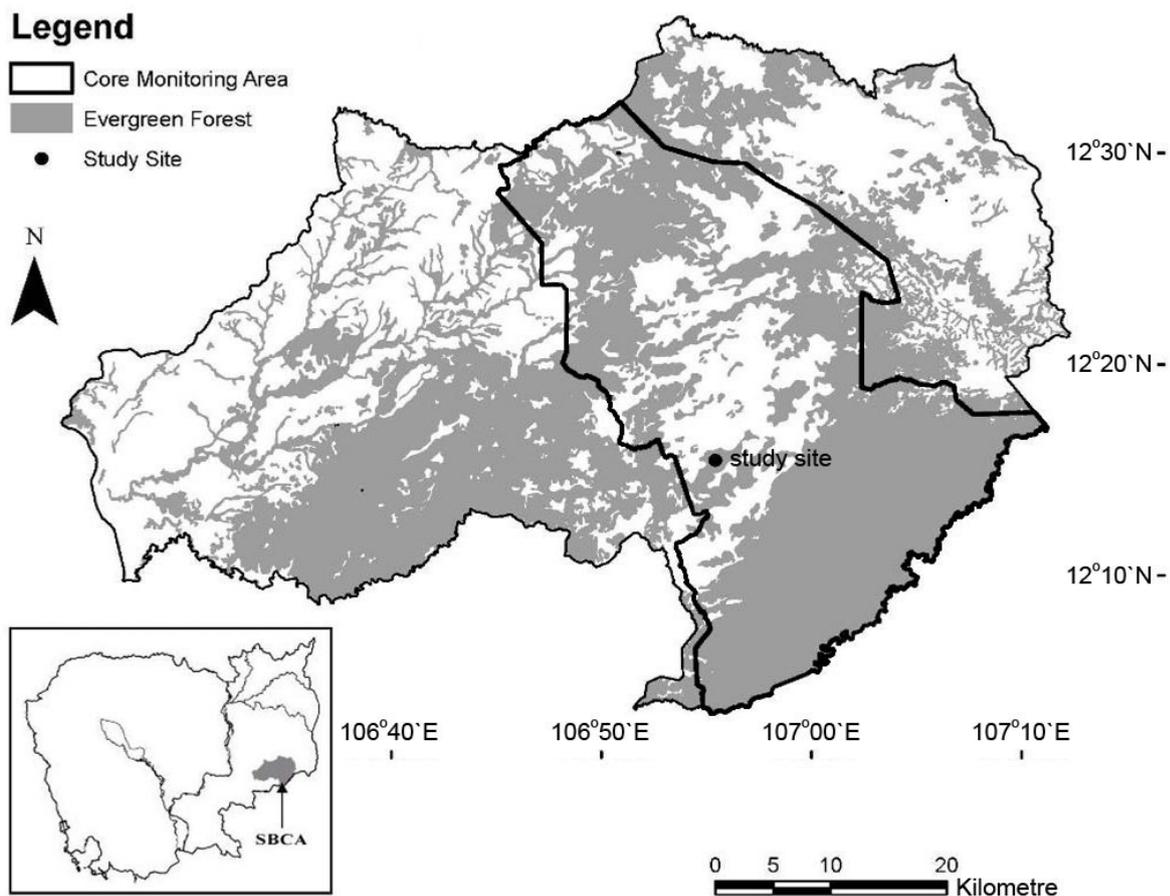
## **Seima Biodiversity Conservation Area**

The SBCA was established in 2002 by decree of the Ministry of Agriculture, Forestry and Fisheries of the Royal Government of Cambodia. The conservation area covers 3,034 km<sup>2</sup>, comprising a core area of 1,550 km<sup>2</sup> in Mondulhiri province and a surrounding buffer zone of 1,484 km<sup>2</sup> in Mondulhiri and Kratie provinces. It is managed by the Forestry Administration with the support of WCS.

The area has a wide range of habitats, from dense evergreen hill forests along the Vietnamese border to extensive deciduous dipterocarp forests in the plains to the north and west. Altitude ranges from 100m a.s.l. in the lowland deciduous dipterocarp forest to >700m a.s.l. on the Sen Monorom plateau.

The complex mosaic of different forest types (Zimmermann and Clements, 2002) at this juncture of two distinct biogeographical regions (the Annamite Mountains and the Indochinese Lowlands), containing many streams, wetlands and mineral licks, supports a high diversity of species at globally significant densities. For example, seven to eight species of primate and seven of cat have been recorded – among the highest figures for

single sites anywhere in Asia. The two most notable features of the fauna are the high number of locally endemic species (see below) and the high number of Globally Threatened species. Many of the endemics are also threatened (Walston *et al.*, 2001).



**Figure 2-1** Map of Seima Biodiversity Conservation Area with locator map of Cambodia and study site, from Rawson *et al* in press.

The local endemic species are mostly restricted to the evergreen/semi-evergreen forests of the southern Annamite Mountains along the Vietnamese border. The SBCA represents one of the most important remaining areas of evergreen/semi-evergreen forest in this region, and so is central to the survival of these species. Key examples of such species include yellow-cheeked crested gibbon (*Nomascus gabriellae*), black-shanked douc (*Pygathrix nigripes*), Germain’s peacock-pheasant (*Polyplectron germaini*) and orange-necked partridge (*Arborophila davidi*).

The site is also a key refuge for many other species that are more widespread but are nonetheless threatened throughout their ranges. Examples from a long list include tiger

(*Panthera tigris*), clouded leopard (*Pardofelis nebulosa*), marbled cat (*Pardofelis marmorata*), sun bear (*Ursus malayanus*), Asiatic black bear (*Ursus thibetanus*), Asian elephant (*Elephas maximus*), gaur (*Bos gaurus*), banteng (*Bos javanicus*), Eld's deer (*Cervus eldii*), green peafowl (*Pavo muticus*), giant ibis (*Pseudibis gigantea*), white-winged duck (*Cairina scutulata*), white-rumped vulture (*Gyps bengalensis*) and several turtle species (Walston *et al.*, 2001).

The area is traditionally home to the Phnong, an upland ethnic minority who have been living in the area for over 2000 years (Evans *et al.*, 2003), although there are also some Stieng communities in the west. These people have a long connection to the area, detailed local knowledge and complex cultural ties to the land as a result of family history, traditional livelihoods and beliefs. Today the Phnong are engaged in low-impact shifting agriculture, chiefly in old fallow areas, together with paddy and cash crop cultivation where soils and markets permit. The collection of forest products is a central part of livelihoods. The most important forest activity is resin tapping, which supplies 40-50% of total livelihood needs in most villages (McKenny, 2001) (see Figure 2-3). Studies have shown that locally used techniques at the current level of intensity have little impact on the health of the forest (Evans *et al.*, 2003), and this is a good example of a product that can be harvested sustainably, linking human benefits to forest conservation. Other important resources include rattan, timber, bamboo and fish.

Currently major threats to wildlife and their habitats include hunting with guns and snares, forest conversion, logging, land grabbing, immigration and economic land concessions. External pressures, such as commercial logging, immigration and land grabbing, have increased considerably in recent years. These also threaten the livelihoods of the local indigenous Phnong and Stieng, principally through loss of the forest habitats that are essential for livelihoods, and the denial of forest resources. The area has been the target for a joint project of the Forestry Administration and WCS since the declaration of the SBCA in 2002. This includes research, law enforcement and land-use planning in co-operation with both the authorities and local communities. These activities have been broadly successful at mitigating many of the major threats to wildlife, habitats and local livelihoods, principally through the maintenance of the forest cover and reduction in commercial hunting pressures. The deforestation rate, based on satellite image analysis, was only ~0.05%/year over the four years from 2001 to 2004

(WCS unpubl. data). With continuing government support it is hoped that the initiative will build on these initial successes to establish a landscape vision for the SCBA.

The SBCA also forms part of a much larger complex of linked protected areas, including four in Cambodia (three Wildlife Sanctuaries and one Protected Forest) and two National Parks in Vietnam. The total area of this group of reserves is greater than 10,000 km<sup>2</sup>, making it one of the largest and most important in South-east Asia. This conservation landscape offers one of the best opportunities in Indochina to preserve viable populations of the largest and rarest mammals.

### ***Primate fauna***

SBCA has a rich diversity of primate fauna, with seven to eight species from four genera found at the site. Populations of several of these species have been shown to be among the most robust within their ranges (Pollard *et al.*, 2007, Clements *et al.*, 2008, Rawson *et al.*, in press).

Members of the subfamily Colobinae confirmed from the site include the black-shanked douc (*Pygathrix nigripes*) and the silvered langur (*Trachypithecus margarita*). A recent taxonomic assessment has suggested that the silvered langurs east and west of the Mekong should be split at the species level, the former representing *T. margarita* and the latter *T. germaini* (Nadler *et al.*, 2005). The former can apparently be distinguished from the latter based on its light coloured eye rings and contrastingly dark hands and feet (Nadler *et al.*, 2005) based partially on genetic and photographic evidence from a captive individual from the site (see Figure 2-4). More field and genetic evidence concerning the distributions of these putative species, especially that the Mekong represents a geophysical barrier, needs to be acquired before the taxonomic affinity of the species at SBCA can be confirmed, but the evidence is suggestive that at least *T. margarita* exists here. Silvered langurs are rarely seen in the southern, more evergreen part of the SBCA and seem to be associated with river systems while black-shanked doucs are associated more with evergreen forests (see Chapter 6) and are by far the most commonly encountered primate species in the area.

- Figure 2-2** Clearance along the Samling road. Photo: WCS/Tom Clements
- Figure 2-3** Collecting resin from *Dipterocarpus alatus* tree. Photo: Ben Rawson.
- Figure 2-4** Captive juvenile silvered langur. Note eye rings and dark hands and feet, characteristic of *Trachypitecus margarita* according to Nadler et al (2005). Photo: Allan Michauld

Photos in printed version

**Figure 2-5** Female yellow-cheeked crested gibbon (*Nomascus gabriellae*). Photo: Ben Rawson/Conservation International

**Figure 2-6** Pygmy loris (*Nycticebus pygmaeus*) splayed and dried. Photo: Ben Rawson/Conservation International

**Figure 2-7** Crossing the O'Mahoit River in the wet season. Photo: Allan Michauld

Photos in printed version

Three species of the genus *Macaca* are found within the SBCA. These are the long-tailed macaque (*Macaca fascicularis fascicularis*), the northern pig-tailed macaque (*Macaca leonina*) and the stump-tailed macaque (*Macaca arctoides*). In undisturbed evergreen/mixed forests, the pig-tailed macaque appears to be the commonest species followed by long-tail macaques and stump-tailed macaques, the latter of which are rarely seen. Macaques are sometimes taken as pets, the more terrestrial species being vulnerable to snaring.

One species of gibbon, the yellow-cheeked crested gibbon (*Nomascus gabriellae*), is found within the SBCA (see Figure 2-5). The species has been the focus of both ecological (Rawson, 2004) and population level (Pollard *et al.*, 2007, Clements *et al.*, 2008, Rawson *et al.*, in press) work at the site. The population seems to be very healthy, with an estimated 809 ( $\pm 83$ ) groups in the core area, suggesting that this may be the most important protected population of this species globally (Rawson *et al.*, in press). While threats appear to be low, the degree of trade into Vietnam of this species is unknown.

The number of species of Strepsirrhini at the site is currently unknown but would be restricted to two at most, the pygmy loris (*Nycticebus pygmaeus*) and the Bengal slow loris (*Nycticebus bengalensis*). In recent years there has been much discussion about the taxonomy of *Nycticebus* in Indochina. For example, all specimens referred to a previously described species, *N. intermedius*, have been found to consistently group with one of the other two in size and pelage (Groves, 2004, Streicher, 2004). The distributions of the two loris species is not clear, although it seems that the range of *N. bengalensis* may not extend as far south as SBCA, meaning that only *N. pygmaeus* would be found here. Further survey work is required to confirm this possibility. Loris are used in the area for traditional medicine, the animals being flattened and dried to be used as a tonic for women who have just given birth (see Figure 2-6).

## ***Camp 6***

Several sites were surveyed before settling on a study site for long-term observations on *P. nigripes*. Camp 6 (UTM 0709277/1356031) is situated on the western bank of the O'Mahoit River in what was designated as Coupe 5 by Samling International at the time the study started. Originally, the intended study site had been located in Coupe 3, an area dominated by evergreen forest close to the Vietnamese border, but the site had to be moved due to lawlessness and death threats. Coupe 5 contains a range of habitat

types, from seasonal meadows, to open deciduous dipterocarp forests, to deciduous through to mixed deciduous, semi-evergreen and evergreen forest types (Walston *et al.*, 2001).

The study site proper largely consisted of semi-evergreen forest, with bands of deciduous forest dominated by *Lagerstroemia cf. calyculata* in some areas and bounded on the northwest by deciduous dipterocarp forest – Shry Plain. Evergreen/semi-evergreen forest was especially associated with rivers and hills at the site. For a detailed discussion of species composition at the site, see chapter 4. Soils in the area “feature poor plinthite podzol soils supporting humid lowland evergreen forests in lowlands areas; and basalt derived regur and latosol soils supporting medium elevation semi-evergreen forests and grasslands on the Chhlong (Mondolkiri) Plateau,” (Ashwell *et al.*, 2004, p 9).

Hunting pressure at the site was apparently quite limited. At no time were snares or other traps ever detected within the study site, and only three gunshots were recorded during the study's duration. There is some indication that the area was avoided because of our near permanent presence in the area, although there were also indications that the trail system and even the camp may have been used on several occasions by hunters when the site was unoccupied. Hunting dogs were seen on several occasions at the site during the study. On one occasion, two sambar deer (*Cervus unicolor*) raced through camp pursued by hunting dogs, although the owners did not appear.

Logging and removal of non-timber forest products was also rarely encountered at the site, with the exception of resin-tapping. Resin-tapping involves cutting a trough in the base of a resin tree – usually *Dipterocarpus alatus* at the site – and stimulating the flow of resin with fire. The resin can then be removed and either utilised locally for illumination, or waterproofing, due to its flammable and oily properties, or more usually sold to middlemen for export. Commercial end uses for resin are likely to be for varnishes and perfumes (Evans *et al.*, 2003). It is a major source of income for the local people, with individual trees owned by families, usually the finders of the trees, although rights can be sold and traded (Evans *et al.*, 2003). Resin-tappers were seen in the area fairly frequently as resin is typically collected every week or two and resin trees were common in the area. A network of small trails facilitates access to these trees. Hunting is generally not done on these trips due to the large amount of resin which needs to be removed (Evans *et al.*, 2003).

Towards the end of the study some individuals apparently hostile to our presence were utilising the area, a no hunting sign was defaced and some 50 phenology tags removed. In general however, relationships with the Phnong people were good, especially as the project and the wider WCS program supported many individuals with jobs as local guides and surveyors.

A wide variety of wildlife was commonly encountered at the site during field activities around Camp 6, including rare mammals such as the Asian elephant (*Elephas maximus*), herpetofauna such as the elongated tortoise (*Indotestudo elongata*) and rare birds such as white-wing duck (*Cairina scutulata*) and greater hornbill (*Buceros bicornis*).

Access to the site involved a one hour drive from base-camp (UTM 0708981/1342325) through Keo Seima village onto a drop-off point at Phum Beng (Beng village) (UTM 0708149/1351421), a small village of some five houses. From there a three hour walk was required to reach Camp 6. Access was possible year round although on occasion one of the two river crossings was unfordable for a few days (see Figure 2-7). The camp itself was very basic, consisting of a small A-frame under which hammocks were slung and tarpaulins could be placed over the top.

In order to facilitate study of the primates at the site, a network of trails was cut through the area which complemented the already existing resin trails (see Chapter 3 for map of site). Trails were cut with the intention of making quiet walking possible without removing saplings and lianas wherever possible. Trails were maintained throughout the year. Viewing distance from trails differed depending on habitat type, with the more evergreen areas having as low as 15 m visibility through the canopy, while in some more deciduous areas it was possible to see up to approximately 80 m.

### ***Weather***

Rainfall was measured daily from 26/10/2002 until 30/9/2004 using a Nylex 500 rain gauge located at the Samling base camp. The difference in rainfall between base and the study site proper is probably minimal given that they are only 13.7 km apart. Temperature was measured hourly at the site from 27/10/2002 until 5/7/2004 using Onset Hobo 2k Temp data loggers which have an accuracy of 0.7° at 25°C. Data loggers were located at Camp 6, 1.5 m above the ground and within a homemade weather shelter. For several months temperature was also recorded in the lower canopy, approximately 10 m above the ground.

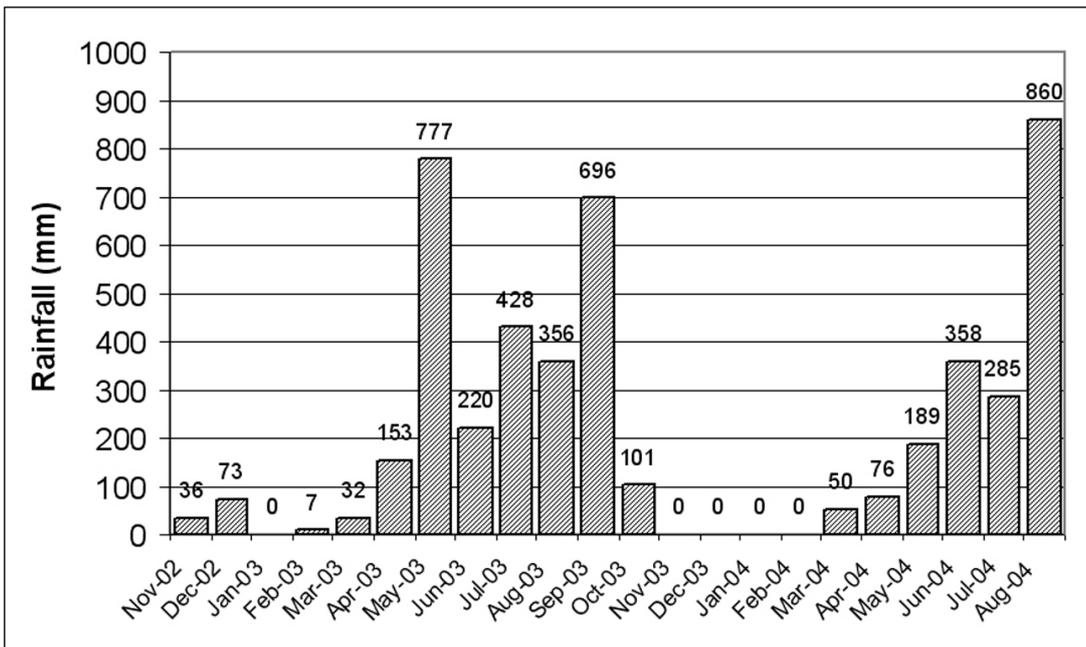


Figure 2-8 Rainfall data from the study site.

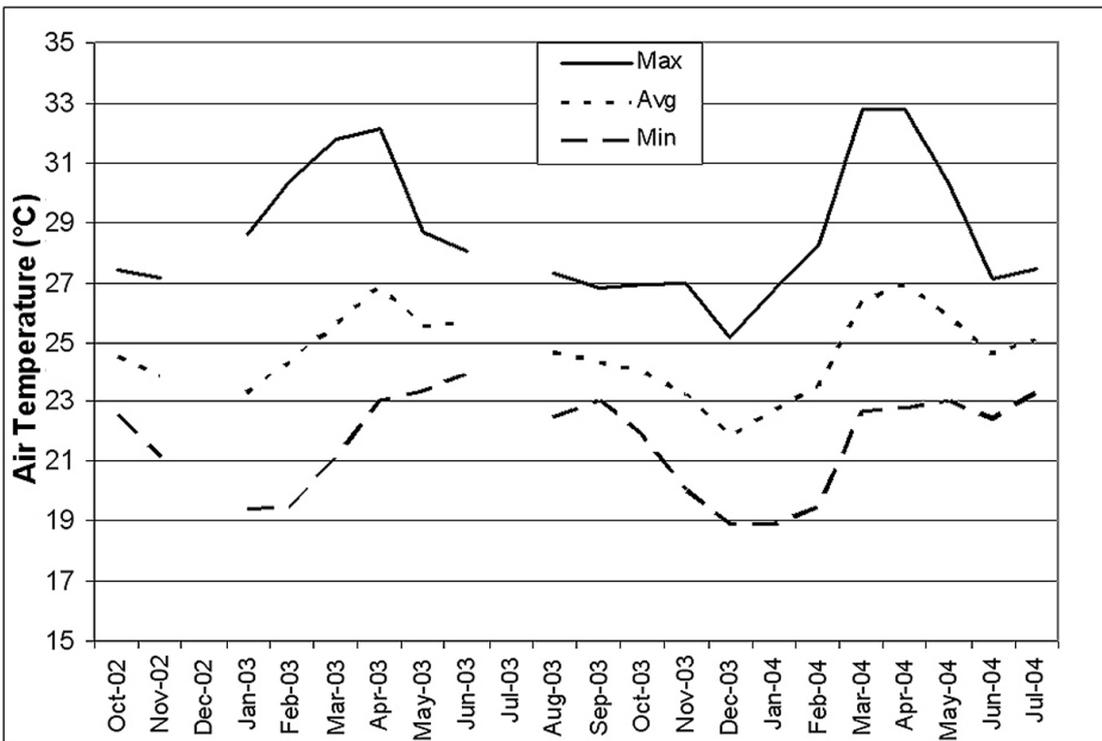
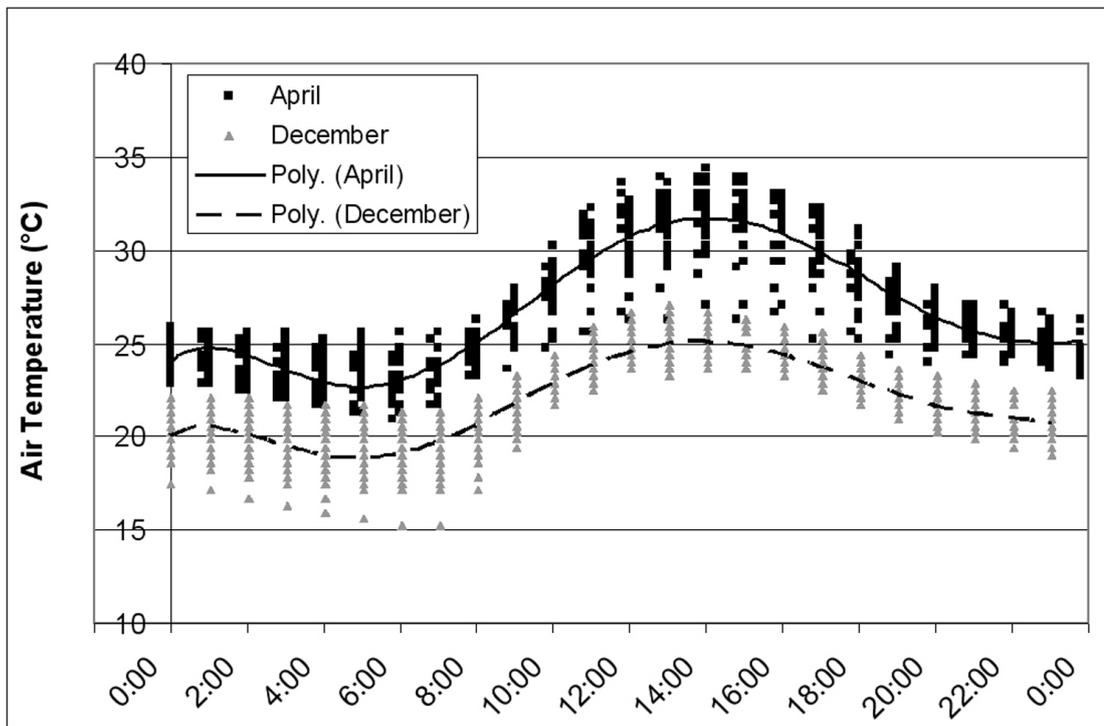


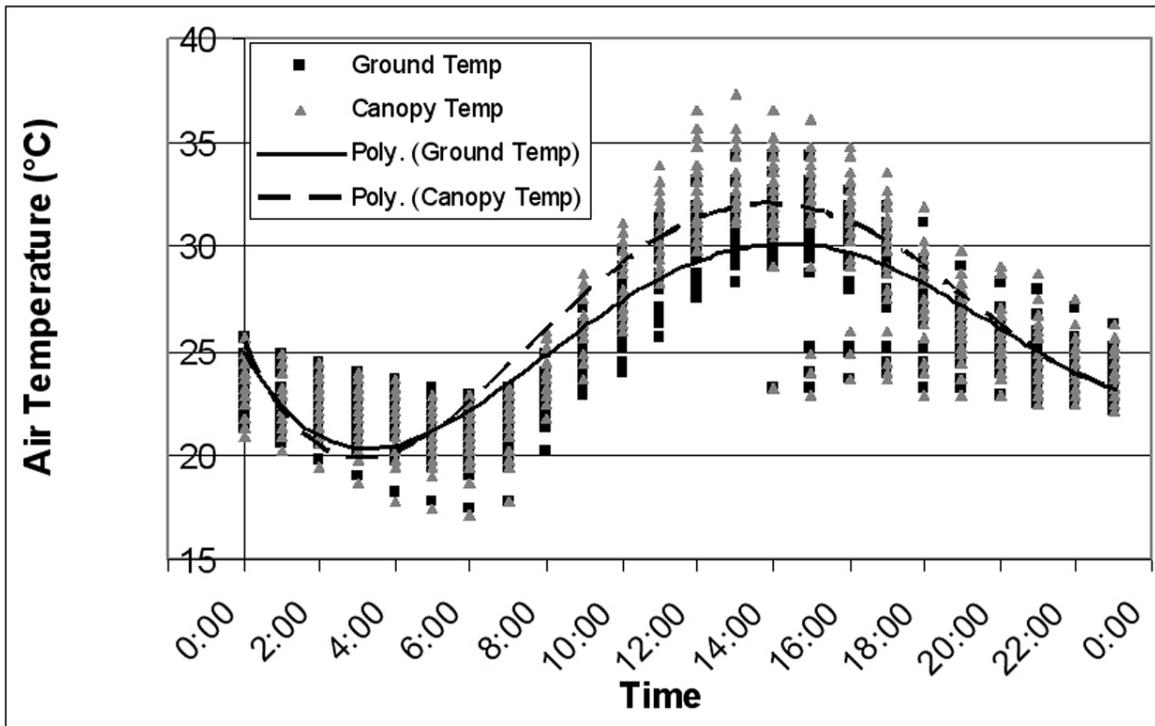
Figure 2-9 Temperature data from the study site.



**Figure 2-10** Daily air temperature and polynomial trend lines for April and December 2003 at Camp 6, respectively the hottest and coldest months of the year.

Data loggers were rotated every month to avoid data loss through batteries running flat and malfunctioning units; despite this there was some data loss due to use of low quality batteries and the removal and partial consumption of one unit by wildlife. Major data loss occurred in December-January 2002 and July-August 2003. All other months are complete except for the starting and finishing months which only have five days each and August 2003 which has only eight days. Rainfall data from the study logged a total of 2770 mm in 2003, the only full calendar year in which data were taken. This tallies well with data from a weather station at Keo Seima Health Centre which averaged 2430 mm between 2000 and 2004 (Nomad RSI unpublished data). The majority of rain falls between the months of May and October, although in 2003 there was also significant rain in April (Nomad RSI unpublished data and see Figure 2-8). Drying months (i.e. those where water loss occurs in the system) are between November and March, with water accumulation occurring from April to October.

Monthly minimum temperatures ranged between 18.86°C (December 2003) and 23.93°C (June 2004), while maximum temperatures ranged between 25.17°C (December 2003) and 32.81°C (April 2003) (see Figure 2-9), making April the hottest month and December the coolest (see Figure 2-10) Average temperature for the year 2003 was 24.6°C, based on 6829 measurements. Little difference in temperature was detected between the lower canopy and ground level although canopy temperature was cooler in the hours before sunrise and hotter during daylight hours (see Figure 2-11).



**Figure 2-11** Daily air temperature and polynomial trend lines at 1.5 m and 10 m above the ground at Camp 6 during March 2003.

## ***Methods***

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This chapter outlines the general methods that were used for data collection and analysis throughout this study. Individual chapters contain more detailed information such as the statistical tests, equations etc. used relevant to that part of the analysis.

### **Study site selection**

As discussed in Chapter 2, the original study site selected for this research was in an area of evergreen forest close to the Vietnam border, then known as Coupe 2 as, based on limited knowledge, this area was thought to have high numbers of primates (Walston *et al.*, 2001); but due to security concerns in this area it was determined that the study site would have to be moved further north into Coupe 5. Assessment of potential areas for setting up a study site was made using 1:50,000 topographic maps which contained some habitat data, but these were published in 1969 and when ground-truthed were found to be not very accurate.

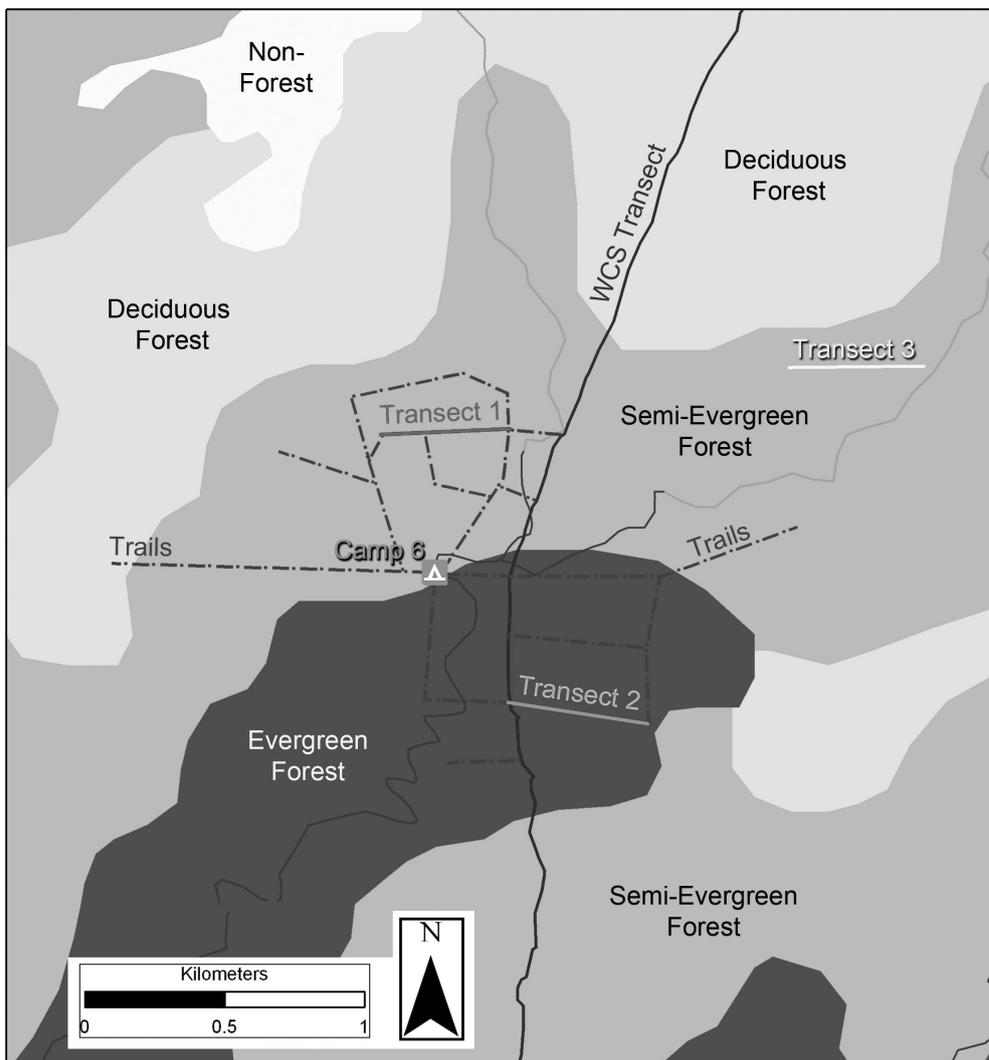
Numerous surveys were conducted in areas assessed to be of potential suitability based on these maps, local informants and previous records of primates. Eventually, the area of forest around what is known as Camp 6 was selected for the study, and Camp 6 became the base camp. This was based on sightings of primates, presence of apparently undisturbed habitat, logistical factors including the presence of a year round water supply for staff, relative ease of access, and lack of permanent settlements in the area. The general study area was then delimited and applicable habitat types for *Pygathrix nigripes* identified. These included semi-evergreen and mixed deciduous forest patches but excluded areas of dry deciduous dipterocarp and meadows. Initially a small number of trails were cut to facilitate movement and to make preliminary assessments of key areas being utilised by the doucs, with the trail system being extended once this had been achieved.

### **Phenology transects**

#### ***Transect setup***

A series of transects was created in order to provide baseline data on plant species diversity and to track plant resource abundance at the site (Figure 3-1). Three 500 m x 10 m phenology transects were cut (although only two were utilised for

phenological monitoring), marked and monitored for a total of 18 months. Transects were used, rather than plots, because transects are more likely to sample patchily distributed species (Ganzhorn, 2003) (which would be expected at the site due to the heterogeneous nature of the habitat), although they do result in greater edge effects (White and Edwards, 2000a). Selected tree methods (Hemingway and Overdorff, 1999) were not used as, prior to this study, there were insufficient data to suggest which tree species would be selected by *P. nigripes*. Further work, however, would do well to include key selected tree species in phenological work in tandem with transects (Hemingway and Overdorff, 1999).



**Figure 3-1** Study site showing camp, transect and cut trail locations and habitat types (JICA, 2003).

The location of the three transects was determined randomly within areas believed to be habitable for *P. nigripes* based on limited survey data (Walston *et al.*, 2001 and

preliminary survey work from this study). Transects were then located randomly within these areas using the Microsoft Excel random number generator to generate UTM northings and eastings. After designating the starting point of transects, the direction the transect would follow was randomly determined using the eight compass points (N, NE, E, SE, S, SW, W, NW) and Microsoft Excel's random number generator feature. If the 500 m transect was judged to have some part outside the habitable forest, then the transect location was discarded and another generated.

Transect start locations were found in the field using a Global Positioning System (GPS) and then trails were cut along the predetermined bearing using a compass. There was found to be some error in this method, and as a result transects were not completely straight. Each transect was 500 m long and 10 m wide, measured using a 30 m tape measure. This gave a total sampling area of 0.5 ha/transect and a total of 1.5 ha across all three transects. All trees and lianas  $\geq 10$  cm diameter at breast height (DBH) were included in transects. Only trees deemed to have half or more of their trunk base within the transect were included in that transect to avoid edge effects (White and Edwards, 2000a). Each tree was recorded as to its distance along the transect, and its distance to either the left or the right of the centre line. In total, Transect 1 contained 188 trees and lianas, Transect 2 contained 237 and Transect 3 156, for a total of 581.

Trees were all marked with an aluminium tag which had the transect number and three digit tree number etched into it. For example, tree number 105 on Transect 1 was marked TRAN1-105. Trees were also marked with a red spray painted cross in order that those which lost their tags could easily be identified as belonging to the transect. There were several instances of tags being removed from trees during the period of study: some were chewed to pieces, probably by civets; some removed by elephants; and, at one stage, half of one transect had all its tags removed by disgruntled poachers. Using the contextual information all these trees were identified and re-tagged.

### ***Tree measurements***

The height of all transect trees was measured using a "Ranging TLR75" range finder, the accuracy of which was questionable. We determined, by measuring horizontal distances, that accurate measurements with the range finder were limited to between c10 m and c25 m. This inaccuracy precluded using the range finder for determining heights using Pythagoras' Theorem (using measurements of distance from observer to tree base and observer to tree top), as the hypotenuse was usually further than 25 m.

Instead, we would stand under the tree and take a reading to the highest point visible, adding standing height to the total. A great deal of effort was made to position ourselves where the highest part of the tree could be seen, but there is doubtless some error in these measurements. It was deemed inappropriate to cut down a sample of trees to test height estimations (Gumal, 2001), so whether measurements are generally underestimated or overestimated is unknown. For trees less than 10m, height was estimated using a measured 3.5m stick as a guide.

Each tree included in the transects had its diameter at breast height (DBH) measured. Only trees that had a DBH  $\geq 10$  cm were included. There is some variation in the literature as to the exact height that DBH actually represents, with different researchers using 1.2 m (Chapman *et al.*, 1992), 1.3 m (Miller and Dietz, 2004, White and Edwards, 2000b, Lewis *et al.*, 2004), or 1.5 m (Dold *et al.*, 2000), some texts even being internally inconsistent (White and Edwards, 2000a). This study used the more standard and intermediate height of 1.3 m. All measurements were made with a standard tape measure giving the tree's circumference which was later converted to DBH by simply dividing by  $\pi$  (3.1416). Where trees were buttressed measurements were taken above the buttresses where possible, otherwise between buttresses, and DBH then estimated. In cases of sloping topography, DBH was measured from the lowest point of the tree. If a tree had multiple stems, it was included only if one of its stems  $\geq 10$  cm DBH, in which case all stems were measured for later estimates of basal area.

Basal area was calculated for all transect trees using DBH measurements. Tree stems were treated as cylindrical; DBH was halved to find the radius ( $r$ ) and then the formula  $\pi r^2$  applied to arrive at basal area (White and Edwards, 2000b). Basal area of trees with multiple stems was calculated by summing the areas of all stems.

### ***Tree identification***

Botanical work in Cambodia is hampered by lack of skilled professionals, a herbarium or field guides. The country's educated elite, forestry facilities and libraries were destroyed in the 1970s by the Khmer Rouge, and as yet these have not been replaced (McDonald, 2003). As a result, botanical identification followed a piecemeal approach, starting with identifications by local informants in Khmer, translation to scientific names, and then double checking identifications with field guides where said species were included. Samples were taken where possible from trees on transects as they fruited or flowered, preserved in 70%-90% alcohol and later pressed and dried using a

gas powered drying machine. A subset of samples was also identified, after the study, by trained botanists.

Original tree species identification was done by a local informant of Phnong ethnicity, Mr. Kruet Cheun, who was deemed to be the most knowledgeable individual on tree identification in the area. Although the Phnong have their own language (also called Phnong), Khmer is spoken widely and fluently and it was in this language that discussions were held. Occasionally the names of trees were known in Phnong but not in Khmer. In order to reduce error in identification it was agreed that it would be better if Mr. Cheun did not identify a tree rather than get it wrong, and indeed he seemed to have no difficulty in admitting that he did not know the names of particular species.

The original identification process resulted in the provisional identification in Khmer of 341 of the 425 trees, or 75.5%. As each tree was given a Khmer name the *Dictionary of Plants Used in Cambodia* (Dy Phon, 2000) was consulted to find the corresponding Latin name. There are, of course, difficulties with this approach as local names may change from region to region. In order to check the validity of the original Khmer identification and the regional translation, a species' name was checked in Gardner's *A Field Guide to Forest Trees of Northern Thailand* (Gardner *et al.*, 2000) and the identification either discarded or provisionally accepted. Because the majority of plants at any time do not have fruit or flower to facilitate identification, most could not be positively identified using this method at that time.

Various double checks on these identifications were run throughout the project. Different locals were employed as guides at different times, and this circumstance was also utilised to check original identifications; it became clear which species were well known and reliably identifiable. Also, while doing monthly phenology checks, identification guides were re-consulted as species came into fruit or flower, and species' identity confirmed or updated if necessary. Samples were also taken at this time, and treated as previously described. Fruits with high moisture content were usually bottled in alcohol rather than dried, for greater ease of comparison throughout the study.

Identifications on a limited set of dried samples were performed by a trained botanist, Andy McDonald (AM), residing in country. Most field identified specimens were found to have been correctly identified and some previously unidentified samples identified, although the process was once again frustrated by lack of in-country resources. At the

end of the study, all non-sterile samples were sent to David J. Middleton (DJM) of the Royal Botanic Gardens, Edinburgh, for identification and housing. This resulted in some additional positive identifications.

Decisions about the final identification of transect trees (Appendix 1) and feeding trees (Chapter 7) used throughout this study took a multi-tiered approach. Firstly, all samples that were identified by DJM and/or AM were considered as confirmed. If these matched the field identifications made either by Mr. Kruet Cheun or the author, then these were considered to be species reliably identified and all field identifications were considered confirmed. Those species that were only identified by field observations were considered to be provisionally identified. These trees are listed in Appendix 1 with standard binomial nomenclature preceded by “*cf.*”

### ***Phenological monitoring***

Of the three transects originally cut and marked, only Transects 1 and 2 were used for long-term monitoring of phenological cycles. Transect three was excluded from the study because data relating to tree heights, stem density and basal area (see Chapter 4) showed it to be located in highly disturbed habitat. As this study’s aims did not include assessment of *P. nigripes* in such disturbed habitat, monthly phenology walks were not conducted on Transect 3, and the area was excluded from the study in general.

While the general recommendation for monitoring of phenology transects is that they should be walked twice per month (Ganzhorn, 2003), in this study walks could only be conducted once per month due to lack of personnel and the large amounts of time required. Phenology Transects 1 and 2 were walked, usually between the 25<sup>th</sup> and the last day of the month, from January 2003 until June 2004. In March 2003 only 129 trees from Transect 2 and none from Transect 1 were monitored and no monitoring was done in November 2003 due to the author’s illness. Thus a total of 16 months’ phenology data were collected over the period of the study.

All monitoring work was either done by or supervised by the author, thereby removing inter-observer error. In terms of intra-observer error, it would be expected that my early observations would have been more likely to miss fruits and flowers than later observations when I had become more experienced and more familiar with the trees of the region. However, data from the first three months of the study actually contained slightly more sightings of fruits and flowers than the same three months after one year’s

experience, suggesting intra-observer error was minimal. This was probably a result of the very slow pace at which early phenology work was conducted to counter inexperience and ensure accuracy. Error may however have been introduced by the differential visibility of reproductive plant parts at different times of year; the deciduous component of the forest lost its leaves during the early part of the calendar year (see Chapter 4).

During the monthly phenology walks, each tree was checked for the presence of fruits, flowers and leaves in general and young leaves in particular. Where any of these plant parts were absent, the tree was given a score of 0 for that factor, if present then the tree was scored on a scale of 1 – 3 based on its abundance. Abundances were subjectively judged estimates of the relative quantity of the plant part in question, as in most phenological studies (Ganzhorn, 2003).

0. Absent
1. Minimal abundance. Factor is scarce but present.
2. Abundant. Factor is common.
3. Highly abundant. Factor dominates the crown.

## **Feeding trees**

Each tree in which a black-shanked douc was observed feeding was tagged. The tree was given a unique number which was spray painted on the bole, and two lines were also painted around the entire circumference of the trunk at head height. This allowed feeding trees to be seen regardless of one's location in relation to the tree. Loose bark was often removed to increase the longevity of the tagging system. Sightings of half eaten items on the ground or activity in the canopy of a fruiting tree or similar occurrences, were not deemed sufficient evidence to tag a tree. Information provided by locals as to tree species that various primates feed from was noted but was not included in any analysis.

After tagging the tree, its location was determined using a Garmin "Summit" Global Positioning System (GPS) unit. The accuracy of GPS points under canopy was not high, but could usually be reduced to 6 to 15 m with perseverance. Heights of feeding trees had to be estimated as a range finder was not available long-term for the project. As discussed above, estimates can be wildly inaccurate; but the majority of feeding tree

heights (80%) were estimated by the author or Nut Meng Hor, both of whom originally used range-finders to find the heights of transect trees, reducing inter-observer error. Following the protocol for phenology trees, DBH and basal area were measured and an estimate of the abundance of the plant part consumed was made. This followed the same guidelines as abundance estimates made for transect trees (see above).

The approach to tree identification was largely the same as that used for phenology trees. Where necessary and possible, botanical samples were taken from feeding trees for later identification. Identification was often hampered where doucs fed from trees with no reproductive parts, as sterile samples are far harder to positively identify. There is therefore a bias in identified feeding trees towards those that contained fruit and/or flowers.

## **Animal observation protocol**

### ***Equipment used and personnel***

Standard equipment for observational studies was used throughout the fieldwork period. This included Optex 10x30 binoculars and Gerber Montana 7x50 binoculars. Time between samples was monitored using a Sper Scientific observational stopwatch with earpiece which could be set to count down from a predetermined time interval after which a “beep” was made, facilitating accurate scan sampling. UTM location of groups was made using a Garmin “Summit” GPS. All data were recorded on the “Activity Budget” data sheets, which included entries for date, time, observer, sample rate, group tally by age and sex, focal individual’s sex, UTM location, activity code, canopy location, substrate support and additional notes. All behaviour codes were also included on the data sheet to ensure accuracy within and between observers.

Data collection was conducted by a small team consisting of the author, Nut Meng Hor (the project’s counterpart from the Forestry Administration, the site management authority), and during occasional periods of the study, two volunteers, Adam Seward and Mathew Preston. Observation teams were supported by local field guides who aided in finding doucs, tagging trees and cutting and maintaining trails. Personnel usually rotated time in the forest to maximise data collection.

### ***The study animals***

Habituation was never achieved with any of the doucs at the site, and we found no noticeable difference in their behaviour toward observers from the beginning to the end

of the study. Difficulty in habituating doucs appears to be a fairly common problem (Phaivanh Phiapalath and Pongthep Suwanwaree, 2008, J. O'Brien, pers comm). I am not aware of any case where this has been done successfully. Additionally, group fission-fusion (see chapter 6) and short contact times made identification of individual study animals very difficult. With the exception of one small group of doucs, which was seen on a fairly regular basis, no individual recognition was achieved. This study therefore makes no assessment at the level of specific individuals or groups, but is restricted to broader generalisations based on observations of animals that for all intents and purposes are assumed to be independent.

When observed, each individual was given an age class based on appearance and behaviour, and was sexed based on its external anatomy where possible. Infants, juveniles and subadults were usually not sexed, as visibility was usually insufficient to determine this accurately. Age classes were based roughly on those presented by Lippold (1977), although as these detailed descriptions are for red-shanked doucs (*P. nemaesus*), and little to nothing was known of changes in pelage during maturation of black-shanked doucs, I had to develop classifications during the study. The classifications used were as follows:

- **Infant:** an individual that has not been weaned. Indications of an animal's infant status are: spending large amounts of time being carried by its mother; breast feeding; poor locomotion skills; pelage either white (very young) or with reddish shanks and very dark face (older).
- **Juvenile:** immature but moving independently of other animals. Juveniles locomote confidently and tend to play a great deal.
- **Subadult:** an individual that is apparently not physically mature and often noticeably smaller than an adult. Often subadult pelage appears much lighter than adult's. It has a "washed-out" appearance to it. Males have not developed secondary sex characteristics of blue scrotum, red penis and extended whiskers on chin. It was often difficult to distinguish between subadult males and adult females.
- **Adult:** evidently sexually and physically mature. Pelage fully developed. Pendulous nipples on females may indicate previous births. Males will have developed blue scrotum and red penis and chin whiskers.

## ***Behavioural sampling protocol***

It was originally planned that the study would use a scan sampling protocol with a sampling interval of 10 minutes. This is easy on the observer and creates a series of independent samples. However, it became quickly apparent that more than one individual was seldom in clear view; that contact times with the doucs were shorter than 10 minutes on average, precluding more than a handful of samples per encounter (see Table 3-1); and that consequently a sufficient amount of data for analysis could not be gathered during the field period using such a large interval.

Therefore, a focal animal instantaneous sampling protocol was used with an interval of 30 seconds. While this calls into question the independence of samples, short periods between instantaneous samples provides some benefit in that data approaches representing actual time budgets (Martin and Bateson, 1993). The high number of encounters and their short duration, averaging only 7.6 minutes or 15.17 consecutive samples, suggests that independence of samples is not an issue here anyway. Details on behavioural samples collected during this study are presented in Table 3-1.

<b>Behavioural Sampling Data</b>	
# of encounters	295
# of samples	4476
Mean # of samples/encounter	15.17
Mean length of encounter	7.6 ( $\pm$ 13.9) mins
Median # of samples/encounter	8
Median length of encounter	4 mins

**Table 3-1** Number and duration of encounters with black-shanked doucs during this study.

The focal animal selected for observation was the closest visible animal, not including infants. Infants were generally excluded from sampling as they were not considered relevant for the main focus of the study, i.e. feeding ecology. The first observation on each new focal animal was taken at the next 30 second mark. The selected focal animal remained the focal until one of the following two conditions was fulfilled, either:

- it was “out of sight” for five sample periods (maximum 2½ minutes)  
or
- it was clear that the original animal could not be sampled further (e.g. had left the area).

In these situations sampling would move to the next closest individual. No maximum time limit was set on taking observations from a single animal but in practice this very seldom exceeded one hour ( $n=4$ ).

## ***Ethogram***

All behavioural activities were divided into mutually exclusive categories and coded for ease of entry into data sheets. Codes were originally based on a wide range of other studies and then adapted for the particular conditions and target species as these became apparent in the early stages of the research. Categories, codes, and their operational definitions are laid out below.

### **Behavioural categories**

#### **Inactive**

*Inactive* (r) – when the focal animal was performing no overt action it was said to be inactive. This was divided into two sub-categories, resting and scanning.

- Resting (r) – if focal animal was performing no overt actions. This included sleeping.
- Scanning (sc) – vigilance behaviour. If the focal animal actively scanned the surrounding area, whether it was the sky in response to large birds, the canopy in response to other primate activity, or the ground. Because of confusion between observers of the exact definition of this category, only data collected by the author were included in analysis of this variable.

#### **Feeding**

*Feeding* (f) – actively eating. This includes removing or manipulating leaves/fruits/flowers etc. in order to consume them, and chewing. Where possible, the item or the part thereof that the focal individual was consuming was also noted. These fell into the following categories:

- Fruit (f) – any fruits where the focal animal was not deliberately targeting seeds for consumption.
- Seeds (s) – any instance where the focal animal was feeding from a fruit but deliberately targeting seeds for consumption, usually made obvious by the manipulation of the fruit and the discarding of other parts.
- Leaves (l) – Simply leaves. These were further divided into two categories based on maturity.
  - Immature (i) – usually made obvious by smaller size than mature foliage, terminal position on branches and/or lighter or redder colour.
  - Mature (m) – usually made obvious by larger size, position and/or darker colouration than young foliage.
- Flowers or flower buds (b) – unopened or opened flowers.
- Figs (fg) – these were considered separately from fruits because of their unique role in tropical forests as providers of large amounts of fruit which probably function as a keystone resource for many species. Separating them allowed discussion of their possible role in *P. nigripes* feeding ecology.
- Other (o) – This was simply included to add any additional categories that had not been covered by those above, with notes made of the food type when the category was used.

## **Travelling**

*Travelling* (t) – movement of the focal animal from one location to another. This could involve relatively short movements of a metre or so to continuous travel bouts. Travelling behaviours were divided by the type of locomotion used, as follows:

- Quadrupedal (q) – any movement where all four limbs were used for locomotion on a substrate, excepting purely vertical movement which was classified as climbing.
- Brachiate (br) – any movement which relied on forelimb suspension.
- Jump (j) – any movement where the focal animal used its hind limbs to spring from one location to another, often used for moving between trees.
- Climb (c) – any movement involving purely vertical movement. Achieved with all four limbs but qualitatively different from the defined quadrupedal movement in

that limbs were used to pull the individual up (or down) and is not a loping gait for vertical movement.

- Drop (d) – any vertical movement down, which at some point involved a loss of contact between the focal animal and a supporting substrate. This was often achieved by the lowering of the body by the forelimbs below the level of the substrate and then dropping into the canopy below.

## **Social**

*Social* (s) – was a category used for documenting social behaviours between individuals.

- Vocalising (v) – any vocal behaviour.
- Groom Other (gx) – the focal animal grooms another individual.
- Groomed by Other (xg) – the focal animal is groomed by another individual.
- Play (p) – the active engagement by one individual with another in an apparently fun and pointless activity.
- Copulate (cop) – self explanatory.
- Disputing (d) – any altercation which involves displays such as lunges, baring of teeth, rapid display locomotions etc. These were split into two categories:
  - Intra-group (in) – altercation between members of a single group.
  - Extra-group (ex) – altercation between members of separate groups.

## **Other**

*Other* (o) – used for behaviours that did not fall into those wide reaching categories outlined above:

- Autogroom (a) – focal animal grooms itself. Scratching was also included in this category in addition to directed removal of parasites or other debris from the body of the individual.
- Defecate (d) - self explanatory.
- Urinate (u) – self explanatory.

## **Out of sight**

*Out of Sight* (os) – was the code used when the animal was not visible or was not sufficiently visible to determine which activity it was performing. As mentioned above, up to five consecutive sample periods where the focal animal was out of sight were generally required before a new focal animal was selected.

## **Forest use**

For each instantaneous sample, a note was also made of the strata of the canopy the individual occupied and the kind of support that was being used in the activity. Definitions of these are laid out below.

## **Canopy usage**

The canopy in the forest seldom exceeded 30 m so canopy usage was divided into the following categories. All data on the focal animal's height in the canopy were estimated.

Lower      0 – 10 m

Middle     10 – 20 m

Upper      20 – 30 m+

## **Support usage**

For each activity the type of support that was used by the focal animal was recorded. These were classified as one of the following four types.

Bole        an upright trunk, the main stem.

Bough      a large branch, 30 cm or more in diameter.

Branch     less than a 30 cm in diameter down to 5 cm in diameter.

Foliage     any support less than 5 cm in diameter.

## ***Detecting P. nigripes groups***

Daily surveys to detect douc groups were conducted on a range of trails cut and maintained especially for the purpose (Figure 3-1). Decisions about which trails to follow on a particular day were determined on an *ad lib* basis. Often it was possible to make a good estimate of where groups might be found, based on previous days' encounters and time of year, and to select a survey route accordingly. If more than one survey group was active, then the two groups of observers would discuss planned routes

before leaving camp to avoid disturbing each other and doubling up on observational data. Time spent surveying differed from day to day and depended on weather, time required for other activities such as trail cutting/maintenance and phenology, and day length. Surveys typically began at 5:30 am and concluded at 5:00 – 6:00 pm, depending on light availability. Because full-day-follows were never achieved and contact with groups until the end of their period of activity was very rare, contact with groups generally had to be established afresh every day.

Despite this, black-shanked douc groups were detected on most survey days and the species was the most commonly seen mammal in the area. Encounter rates were 0.68 encounters/survey hour or conversely 1 encounter/1.47 survey hours (386 encounters from 586.59 survey hours from 81 recorded survey days). When surveying, we walked at a slow speed, approximately 1 km/hour, and made frequent stops to listen for sounds of primates jumping between trees. This was the most common form of detection (61.62% of detections). Being stationary also made it easier to detect movement in the canopy and this proved an effective method of detection (24.24% of detections). The low frequency of vocalisations amongst the doucs and the dense foliage made direct detections of animals very rare (3% and 11% respectively).

Detection Method	Frequency	Percentage
Visual – Foliage	24	24.24%
Visual – Animal	11	11.11%
Aural – Foliage	61	61.62%
Aural – Animal	3	3.03%

**Table 3-2** Relative frequencies for various forms of detection of black-shanked doucs.



## ***Vegetation and phenology***

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### **Introduction**

Having an understanding of primate-plant interactions is an important part of socio-ecological studies. Primate feeding ecology, for example, is intimately linked with botanical compositions of the forest that primates live in, and the phenological cycles these plant species go through (e.g. Leighton and Leighton, 1983, van Schaik *et al.*, 1993, Dasilva, 1994). Because primates rely on these resources for sustenance, bottlenecks and times of abundance in these resources can intimately shape primate ecology (Terborgh, 1986, van Schaik *et al.*, 1993). For example, temporal changes in resource abundance may impact ranging behaviour while variation in spatial abundance may be a factor in maximum group sizes (Clutton-Brock, 1977, Janson and Goldsmith, 1995, Gillespie and Chapman, 2001, and see Chapter 6).

Further, plant species composition and broad habitat typologies can determine primate distribution, abundance and carrying capacity. For example, the dry deciduous dipterocarp forests of Cambodia are unsuitable for gibbons, acting as a dispersal barrier (Srikosamatara and Doungkhae, 1982, Traeholt *et al.*, 2006), a factor which does not impact distributions of long-tailed macaques. Primates may specialise in exploiting certain plant species also, for example colobines often target the Legumes (e.g. Curtin, 1980, Davies, 1991, Dasilva, 1994 and Chapter 7) while gibbons in many locations rely heavily on figs from the family Moraceae (MacKinnon and MacKinnon, 1980, Palombit, 1997). Relative abundance of these key resources may affect the carrying capacity of the forest. Understanding which resources primates rely on can also have conservation implications, for example, frugivorous primates or those with a non-diverse diet may be more susceptible to selective logging regimes (Johns and Skorupa, 1987).

A key approach to understanding primate-plant interactions is to monitor forest phenological cycles. Phenology is the study of temporal patterns and changes in the fruiting, flowering and leaf production of plants (Ganzhorn, 2003). Very few plant species show continuous fruiting, flowering or new leaf growth in even the most constant of conditions (van Schaik *et al.*, 1993). Rather, some species flower and fruit regularly, some at irregular intervals, some species produce leaves continuously while at

the other end of the spectrum some have long periods of leaflessness (Whitmore, 1984). By extension, forests, being composed of many different species, have a range of different phenologies occurring simultaneously, and as a result the total abundance of each of these phenophases is in a state of flux. The current chapter describes these seasonal changes in phenophases and the abundance of different plant parts which are then linked with *Pygathrix nigripes* feeding ecology data in Chapter 7.

Floristically speaking Seima Biodiversity Conservation Area (SBCA) lies within the Central Indochina Dry Forests, an area of relatively flat topography, mostly below 200 m above sea level (ASL), which is dominated by open, deciduous dipterocarp forests, with occasional extensive patches of semi-evergreen forest in wetter regions (Baltzer *et al.*, 2001). Within these dry forests the study site is located within Cambodia's northeast bio-region, an area which is still dominated by dry deciduous forest, but with fairly extensive sections of humid semi-evergreen forest, most notably in Virachey National Park in the far north, and in southern Mondulhiri Province (Ashwell *et al.*, 2004).

The study site proper is on the southern edge of these forests in Mondulhiri, where intergradation occurs between the dry forests of Cambodia and the southerly section of the Greater Annamite region, an area which is dominated by evergreen and semi-evergreen forests. The division between these two eco-regions is one of gentle gradation, with a change in forest type being evident from the more south-easterly, higher altitude areas (up to c.600 m ASL), which are predominantly semi-evergreen and evergreen forest, to the more north-westerly low altitude areas, which are dominated by deciduous dipterocarp forest (Walston *et al.*, 2001). The study site is essentially within the most northerly extent of this largely contiguous semi-evergreen forest running down from the Sen Monorom Plateau.

While the primary aim of the floristic and phenological research at the study site was to provide a context for interpretation of *P. nigripes*' feeding ecology, a secondary objective was to better describe, quantitatively and qualitatively *Lagerstroemia* dominated semi-evergreen/mixed deciduous habitats, so that more meaningful comparisons than current habitat typology allows might be drawn by researchers and conservationists working within the areas. Towards this end, fairly detailed discussions of forest structure and phenology are presented in this chapter.

## Methods

This section only outlines statistical methodologies utilised for analysis of vegetation and phenology in this chapter. See Chapter 3 for general details about protocols for all measurements made on trees, the locations of phenology transects, phenological monitoring, tree identifications; and Chapter 2 for details on the collection of temperature and rainfall data.

Comparison of tree heights between transects required values to be log transformed to fulfil assumptions of normality; they were then compared using one-way ANOVA using the General Linear Model. Post-hoc testing of difference between transects was calculated using Bonferroni's correction. Comparisons between transects of tree basal area and diameter at breast height (DBH) were performed using the Kruskal-Wallis Test as data could not be normalised. Comparisons between the heights, DBH and basal area of lianas was compared using the Mann-Whitney *U*-test as a small sample size from Transect 3 precluded using the Kruskal-Wallis Test. In order to avoid a Type 1 error caused by multiple tests, significance was set at  $p < 0.01$ .

Importance Value Indices (IVI) were calculated for all trees on Transects 1 and 2 to determine the relative dominance of each tree species within the habitat. IVI were calculated following Blanc *et al.* (2000), where the IVI is the sum of relative density  $D_i$  and relative basal area  $G_i$ , for species  $i$  on each transect, where the sum of all species' IVIs in one transect equals 200. The following equation was used:

$$\begin{aligned} IVI_i &= D_i + G_i \\ D_i &= (n_i / n) * 100 \\ G_i &= (g_i / g) * 100 \end{aligned} \quad \text{Equation 4.1}$$

Comparisons of relative degree of fruiting, flowering, new leaf production and deciduousness between transects and within transects between years was performed using Wilcoxon's test for matched pairs. These could only be conducted on the six months from January to June as these are the only months studied in both years and were performed on figures combined from both transects unless otherwise specified. Because of the small sample size, any overlap in figures yielded a result of no significance for these tests.

Comparisons of mean heights of fruiting and non-fruiting and flowering and non-flowering trees were performed with *z*-tests on log transformed values after testing for normality and homogeneity of variance. Comparisons for basal area on these variables were conducted using the Mann-Whitney *U*-test as data were not distributed normally.

Tests for correlation between phenophases and environmental variables were performed using Spearman Rank Correlation Coefficient. For environmental variables, mean values for November-December were calculated, and used as only one value was available for phenology data.

Comparisons of fleshy and wind dispersed fruits were done by giving each species an index for each month based on the proportion of fruiting individuals, including only individuals that fruited at some time during the study. Frequency for each month was then calculated for fleshy and wind dispersed fruits, and compared with rainfall to determine whether different temporal cycles in fruit types were related to weather using Spearman Rank Correlation Coefficient.

Solar angle data were determined from the computer program ‘Solar Tool’ created by SQUARE ONE RESEARCH PTY LTD. This program can be downloaded from <http://www.squ1.com>. Data for day length were calculated using a program developed for application in crops by Howard Rawson. All statistical analysis was performed with the statistical software packages SPSS for Windows 11.5.0 or MINITAB 13.20 on a PC.

## **Results**

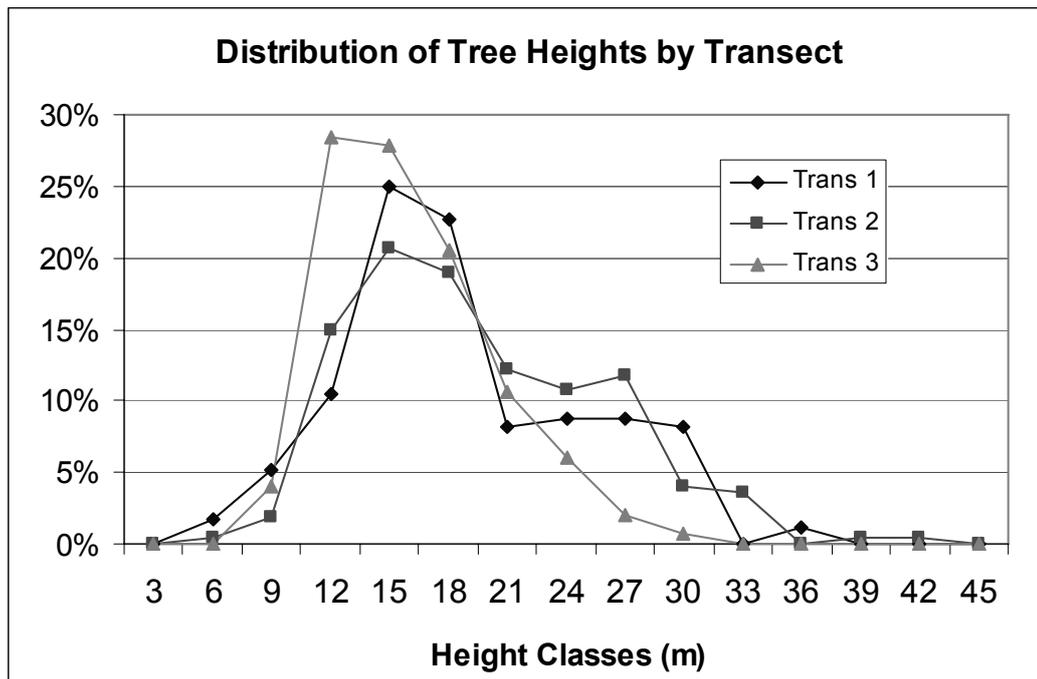
### ***Forest structure***

#### **Height**

Three transects were cut (two of 500 m x10 m and one of 300 m x10 m) in order to monitor phenological changes in the forest (see Figure 3.1). Heights of all trees  $\geq 10$  cm DBH on phenology transects were measured using a “Ranging TLR75” range finder. Lianas and broken stems were excluded, leaving  $n = 545$ , being 172 trees from Transect 1, 222 trees from Transect 2 and 151 trees from Transect 3. Mean height for Transect 1 was  $16.8 \pm 6.1$  m,  $17.7 \pm 6.2$  m for Transect 2 and  $14.1 \pm 4.3$  m for Transect 3.

While the distributions of tree heights are fairly similar for Transects 1 and 2, Transect 3 showed much higher frequencies of smaller trees and lower frequencies of taller trees (Figure 4-1). The percentage of trees 10–20 m tall was 63% for Transect 1 and 64% for

Transect 2, but Transect 3 had almost 80% in this size class. In the 20-30 m bracket, Transect 1 had 28.5%, Transect 2 had 31.5%, while Transect 3 had only 10.5%.



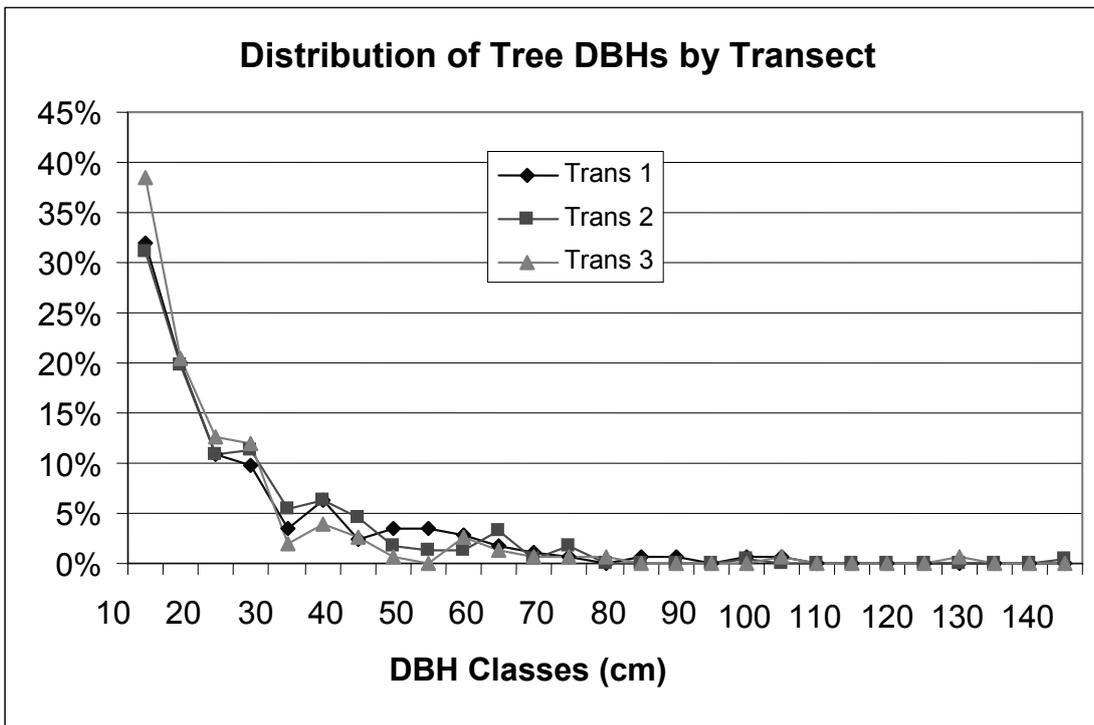
**Figure 4-1** Distribution of tree heights (m) by transect. Lianas and broken stems excluded.  $n = 172$  (Transect 1),  $222$  (Transect 2),  $151$  (Transect 3).

Of the five tallest trees across all transects, Transect 2 contained three, Transect 1 contained two, and Transect 3 contained none. The tallest tree was a specimen of *Dolichandrone* sp. at c.40 m (Transect 2), followed by an unknown species (ពពេជ្រខ្មែរ in Khmer) at c.36 m (Transect 2), an *Anogeissus acuminata* at c.33 m (Transect 1), a *Bombax anceps* at c.32 m (Transect 1) and another unknown species (បង្កើត្យា in Khmer) at 32 m (Transect 2). Trees over 30 m at the site were rare however (see Figure 4-1), with mean height from all transects being  $16.46 \pm 5.90$  m.

Tree heights, log transformed, of the three transects were compared using a one-way ANOVA (GLM) to determine whether all transects were relatively homogenous in this aspect. This showed that heights of trees from different transects were significantly different ( $F = 15.97$ , d.f. = 2, 542,  $p < 0.001$ ,  $n_{\text{tran1}} = 172$ ,  $n_{\text{tran2}} = 222$ ,  $n_{\text{tran3}} = 151$ ). A post-hoc test using Bonferroni's correction showed that while Transects 1 and 2 were not significantly different from each other ( $p = 0.35$ ), Transect 3 had significantly shorter trees than either Transect 1 ( $p < 0.001$ ) or transect 2 ( $p < 0.001$ ).

## DBH

Transect one had the largest mean tree DBH from any transect at  $26.4 \pm 17.9$  cm, followed closely by Transect 2 at  $25.7 \pm 17.3$  cm, and  $23.1 \pm 17.0$  cm for Transect 3. The majority of trees from all transects were under 30 cm DBH (Figure 4-2) although Transect 3 showed a slightly higher percentage of these smaller trees at 59% compared to Transect 1 (52%) and Transect 2 (51%). Median DBH was not found to be significantly different between transects ( $\chi^2 = 5.13$ , d.f. = 2,  $p = 0.08$ ,  $n_{\text{tran1}} = 175$ ,  $n_{\text{tran2}} = 222$ ,  $n_{\text{tran3}} = 151$ , Kruskal-Wallis Test).

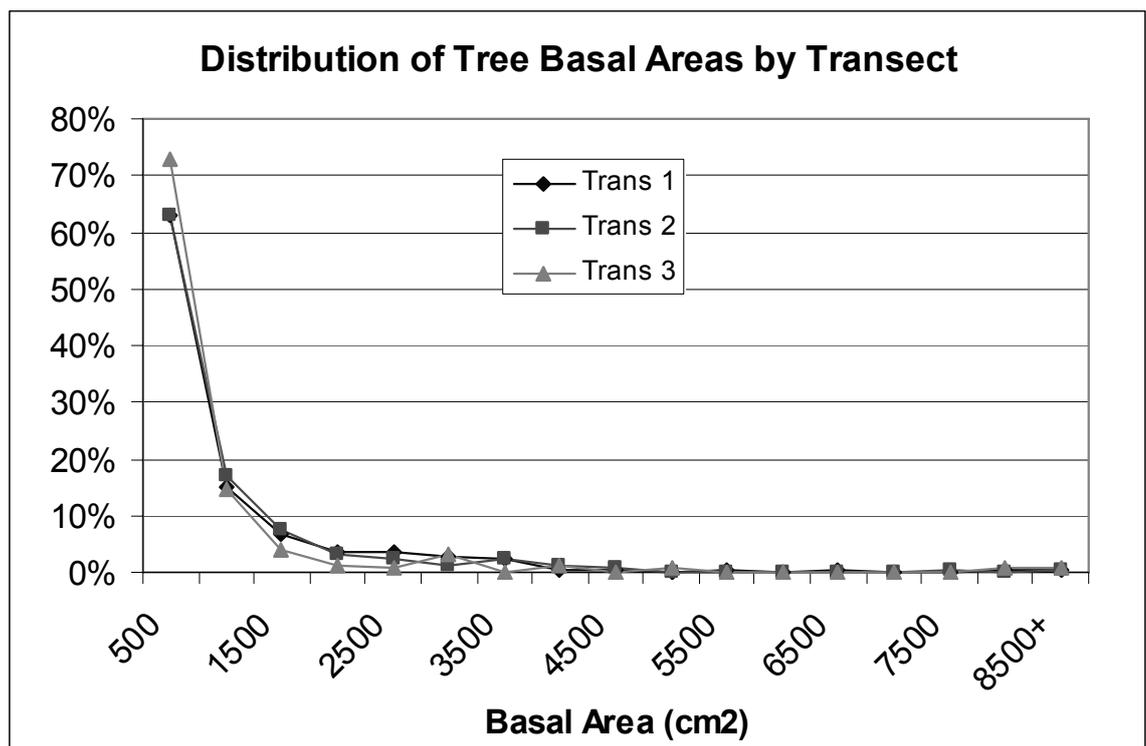


**Figure 4-2** Distribution of tree DBH (cm) by transect. Lianas and broken stems excluded.  $n = 175$  (Transect 1), 222 (Transect 2), 151 (Transect 3).

Of the five trees with the largest DBH, three were from Transect 2, two from Transect 1 and none from Transect 3. The largest, at 138 cm DBH, was a *Millettia* sp. (Transect 2), followed by a *Lagerstroemia cf. calyculata* at 103 cm (Transect 2) as was the fifth at 88 cm (Transect 1), the third largest was an *Anogeissus acuminata* that was also third tallest tree (Transect 1), while the fourth largest at 95 cm was the *Dolichandrone* sp. individual (Transect 2) which registered as the tallest tree on all transects.

### Basal area and tree density

As would be expected from DBH measurements, mean tree basal area for Transect 1 was largest at  $799 \pm 1249 \text{ cm}^2$  followed by Transect 2 at  $753 \pm 1386 \text{ cm}^2$  and Transect 3 at  $646 \pm 1371 \text{ cm}^2$ . Most trees had basal areas under  $1000 \text{ cm}^2$ , 77% for Transect 1, 80% for Transect 2 and 87% for Transect 3e, with very few trees exceeding  $2500 \text{ cm}^2$  (see Figure 4-3). Median basal area was not found to be significantly different between transects ( $\chi^2 = 4.07$ , d.f. = 2,  $p = 0.13$ ,  $n_{\text{tran1}} = 175$ ,  $n_{\text{tran2}} = 222$ ,  $n_{\text{tran3}} = 152$ , Kruskal-Wallis Test).



**Figure 4-3** Distribution of tree basal area ( $\text{cm}^2$ ) by transect. Lianas and broken stems excluded.  $n = 175$  (Transect 1),  $222$  (Transect 2),  $152$  (Transect 3).

When tree basal areas are converted to  $\text{m}^2/\text{ha}$  we can see (Table 4-1) that Transect 2 has the greatest area at  $33.5 \text{ m}^2/\text{ha}$ , followed by Transect 3 with  $32.7 \text{ m}^2/\text{ha}$  and lastly Transect 1 with  $28.0 \text{ m}^2/\text{ha}$ . In terms of tree density however, Transect 3 showed the highest density with  $507 \text{ stems}/\text{ha}$ , followed by Transect 2 with  $444 \text{ stems}/\text{ha}$ , and Transect 1 with  $350 \text{ stems}/\text{ha}$ .

### Lianas

Lianas  $\geq 10\text{cm}$  DBH on transects were also measured and monitored throughout the study period; these totalled 12 individuals from each of Transects 1 and 2, and four from

Transect 3. Analysis of height, DBH, basal area, and density and basal area/ha are presented below (see Table 4-1 for a summary).

Mean liana height was highest for Transect 2 at  $23.9 \pm 3.4$  m, followed by Transect 1 with  $16.8 \pm 6.5$  m and Transect 3 with  $12.7 \pm 6.5$  m. Median height was significantly different between Transects 1 and 2 ( $U = 20, p < 0.01, n_{\text{tran1}} = 12, n_{\text{tran2}} = 12$ , Mann-Whitney  $U$ -test), and Transects 2 and 3 ( $U = 0, p < 0.01, n_{\text{tran2}} = 12, n_{\text{tran3}} = 4$ , Mann-Whitney  $U$ -test) but not between Transects 1 and 3 ( $U = 11.5, p = 0.13, n_{\text{tran1}} = 12, n_{\text{tran3}} = 4$ , Mann-Whitney  $U$ -test). Transect two had the largest median height at 25 m, followed by Transect 1 with 17.7 m and Transect 3 with 15.5 m.

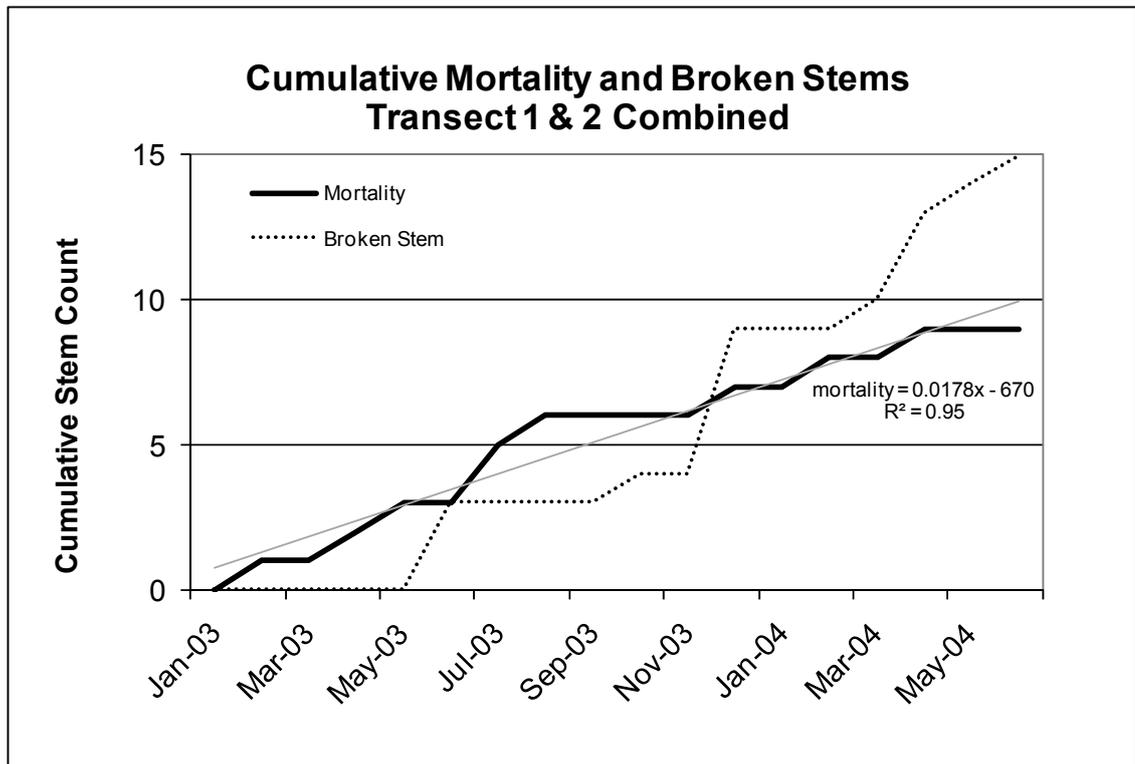
Mean liana DBH for Transect 1 was  $15.0 \pm 9.49$  cm,  $14.5 \pm 3.2$  cm for Transect 2 and  $12.1 \pm 2.6$  cm. Transect two had more large lianas than the other two transects with 41.7% over 15 cm DBH while only 25% of Transect 3's and 16.7% of Transect 1's were larger than this. One liana on Transect 1 was notably large, with a DBH of 44.3 cm. This liana was more than twice the size of the other 27 lianas  $\geq 10$  cm, the reason for this transect's large standard deviation (see Table 4-1). If this outlier is removed, Transect 2 has the highest mean DBH. As with DBH, Transect 1 has the largest mean basal area at  $241 \pm 411$  cm<sup>2</sup>, followed by Transect 2 at  $173 \pm 77$  cm<sup>2</sup>, and Transect 3 at  $118 \pm 53$  cm<sup>2</sup>. Neither median DBH nor median basal area were significantly different between any transects (Transect 1 and 2,  $U = 50.5, p = 0.21$ , Transect 1 and three  $U = 22, p = 0.80$ , Transect 2 and three,  $U = 13, p = 0.18, n_{\text{tran1}} = 12, n_{\text{tran2}} = 12, n_{\text{tran3}} = 4$ , Mann-Whitney  $U$ -test).

Density and basal area per hectare and ratio of trees per liana were also calculated for lianas. Transects one and two show equal highest density with 24 lianas  $\geq 10$  cm DBH/ha, followed by Transect 3 with 13 lianas/ha. Basal area/ha was highest for Transect 1, with  $0.58$  m<sup>2</sup>/ha, followed by Transect 2 with  $0.42$  m<sup>2</sup>/ha and Transect 3 with  $0.16$  m<sup>2</sup>/ha. Ratio of lianas to trees was highest on Transect 2 with a ratio of 1:15, followed by Transect 2 with 1:18 and Transect 3 with only half the density of other transects with one liana  $\geq 10$  cm for every 38 trees.

### **Mortality and tree-falls**

There was some mortality and damage to transect trees during the 18 month study, mainly due to the effects of wind. Nine trees without obvious external damage died during the period of the study, or 2.2% of all transect trees, with an annual death rate of

6.35 trees/ha/year or 1.55% of all trees/year. A cumulative count of trees damaged to the extent that the bole was snapped, removing the entire canopy, during the study totalled 15, or 3.72% of all transect trees, with an annual rate of 10.59 trees/ha/year or 2.63% of all trees/year. The total count of trees seriously damaged or dying during the study was 24, or 5.92% of transect trees, with a rate of 16.94 trees/ha/year or 4.18% of all trees/year.



**Figure 4-4** Cumulative mortality and broken stems of transect trees during the 18 month study period.

Mortality showed no real spatial or temporal patterns, although increases in the number of physically damaged trees generally occurred simultaneously in discrete areas. This was generally due to larger trees falling on nearby trees, damaging them. This was usually caused by high winds.

### ***Forest productivity***

All discussion of forest productivity below is restricted to data collected from Transects 1 and 2. Transect three was not included in monthly phenology walks as after working in the area for several months and upon analysis of structural characteristics presented in Table 4-1 it became clear that this area was quite disturbed, with large numbers of smaller trees and with a very different stratigraphy to either of the other transects. As

the focus of the study was not to compare different disturbance levels this transect and general area were excluded from the phenology study. See Chapter 3 for more detail.

<b>Trees</b>	<b>Transect 1</b>	<b>Transect 2</b>	<b>Transect 3</b>
Mean Height (m)	16.87±6.14	17.71±6.23	14.15±4.15
Mean DBH (cm)	26.42±17.94	25.7±17.36	23.11±17.03
Mean Basal Area (cm <sup>2</sup> )	799±1248	753±1387	646±1371
Density (stems/ha)	350	444	507
Basal Area (m <sup>2</sup> /ha)	28.98	33.47	32.75
<b>Lianas</b>			
Mean Height (m)	16.87±6.55	23.96±3.40	12.75±6.59
Mean DBH Lianas (cm)	14.99±9.49	14.52±3.34	12.08±2.56
Mean Basal Area (cm <sup>2</sup> )	241±411	173±77	118±53
Density (stems/ha)	24.0	24.0	13.3
Basal Area (m <sup>2</sup> /ha)	0.58	0.42	0.16
Ratio of Lianas:Trees	1:14.58	1:18.50	1:37.75
<b>Totals (Trees + Lianas)</b>			
Mean Height (m)	16.87±6.15	18.03±6.27	14.11±4.33
Mean DBH (cm)	25.69±17.73	25.12±17.10	22.83±16.91
Mean Basal Area (cm <sup>2</sup> )	763±1219	724±1357	632±1356
Density (stems/ha)	374	468	520
Basal Area (m <sup>2</sup> /ha)	28.56	33.89	32.90
<b>Mortality</b>			
Broken Stem Rate (per year)	7.1	3.5	NA
Mortality Rate (per year)	4.2	2.2	NA

**Table 4-1** Height, DBH, basal area, density and mortality for trees and lianas ≥ 10cm DBH from all transects.

### Flowering cycles

Patterns in flowering for both transects over 18 months for Transects 1 and 2 are shown in Figure 4-5 below. Overall, Transect 1 averaged 7.44% ± 5.26 of trees flowering each month, while Transect 2 averaged 7.58% ± 5.11. Transects appear to match quite closely in frequency of flowering trees by month and indeed no significant difference between them in flower production was found ( $T = 51$ ,  $p = 0.379$ ,  $n = 16$ , Wilcoxon's test for matched pairs). Peak production occurred in February through April in 2003

with frequencies as high as 16% of all trees in flower for Transect 1 and 15% for Transect 2. This is followed by a precipitous drop in May in both transects and then a second lower peak in June. July through December showed low levels of activity. Peak production in 2004 started earlier than 2003 with January having levels around 10%, that then continued on at generally high but erratic levels until June.

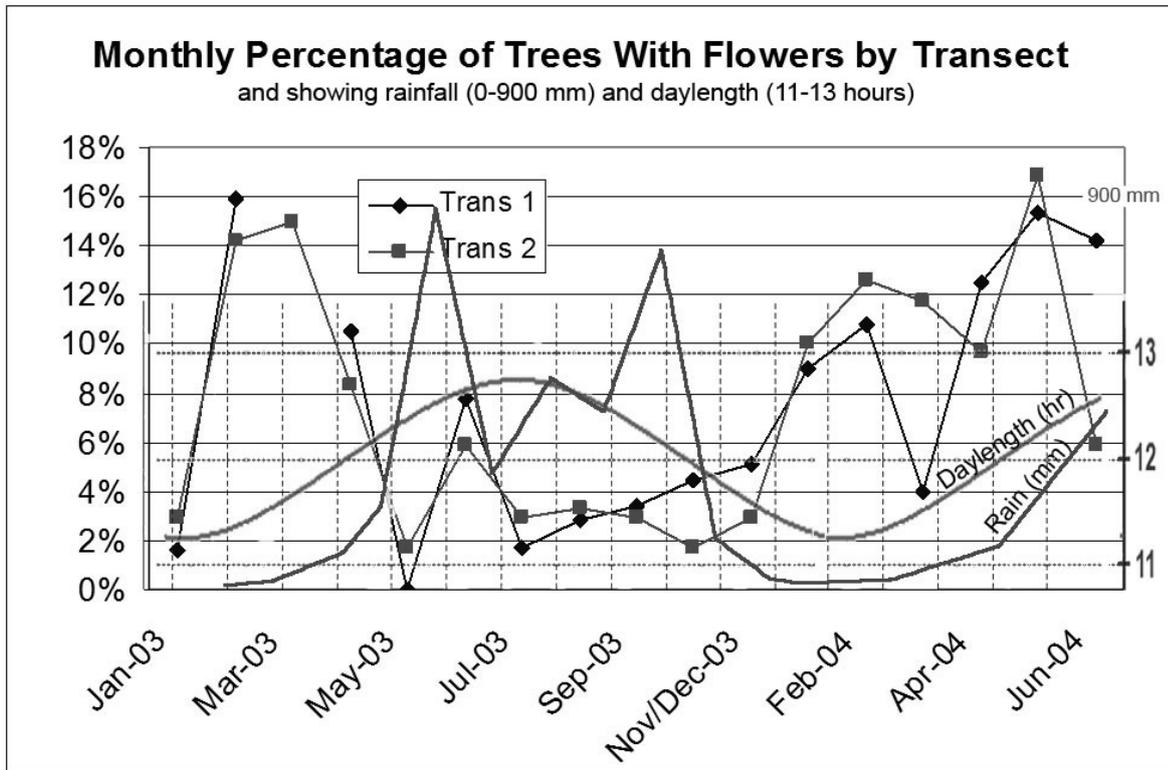
While flowering appears to go on longer and at higher levels in 2004 than in 2003, no significant difference between years for the six months of January through June was found ( $T = 7$ ,  $p = 0.463$ ,  $n = 6$ , Wilcoxon's test for matched pairs). The environmental variables of day length, rainfall and temperature were not found to be significantly correlated to canopy flowering activity (Table 4-).

Over the entire study period of 18 months, 211 of 402 or 52% of trees that survived the full study period flowered. This was similar on both transects, with Transect 1 having 53% and Transect 2 having 52%. Twenty-seven per cent of individuals flowered only once during the study period while 25% flowered twice. Mean height of flowering trees was  $19.4 \pm 6.5$  m, while that of trees that did not flower was  $15.5 \pm 5.0$  m. There was a significant difference between log heights of trees that flowered and those that did not ( $z = 5.848$ ,  $p < 0.001$ ,  $n_{\text{fwr}} = 211$ ,  $n_{\text{nofwr}} = 190$ ,  $z$ -test), with flowering trees being taller. The same relationship is apparent when basal areas are compared, with flowering trees having larger mean basal areas ( $1047 \pm 1680$  cm<sup>2</sup>) than those that did not flower ( $400 \pm 562$  cm<sup>2</sup>), as well as significantly larger median basal areas ( $U = 13340$ ,  $p < 0.001$ ,  $n_{\text{fwr}} = 211$ ,  $n_{\text{nofwr}} = 191$ , Mann-Whitney  $U$ -test).

### **Fruiting cycles**

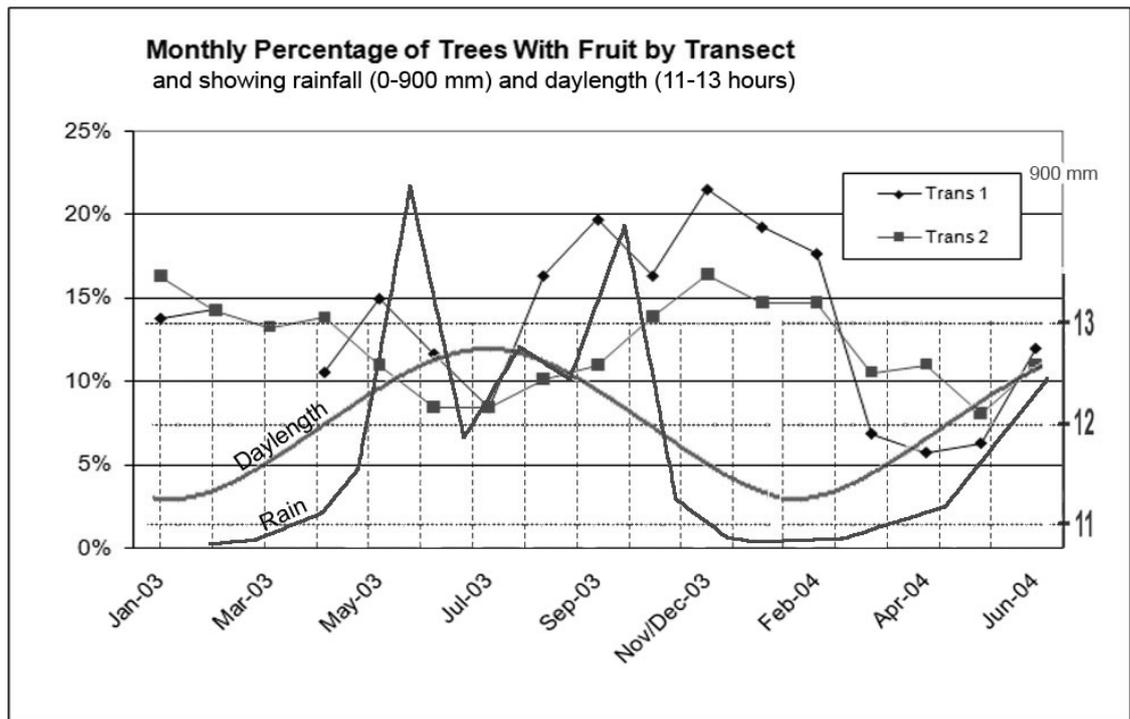
Patterns in fruiting over 18 months for Transects 1 and 2 are shown in Figure 4-6 below. Overall, Transect 1 averaged  $13.4\% \pm 4.9$  of trees fruiting each month, while Transect 2 averaged  $12.1\% \pm 2.7$ . Temporal patterns in fruiting between transects did not seem to follow as closely as either that for flower or leaf production, but transects were not significantly different in fruit production by month ( $T = 44$ ,  $p = 0.215$ ,  $n = 16$ , Wilcoxon's test for matched pairs). Generally, but not exclusively, both showed a peak in production during the dry season, reaching frequencies of 21.5% for Transect 1 and 16.5% for Transect 2, followed by a trough in the wet season with lows of 5.5% and 8.0% respectively. This occurred in both 2003 and 2004 and is reflected in the fact that frequency of trees fruiting is negatively correlated with rainfall ( $r_s = -0.804$ ,  $p < 0.05$ ,  $n = 17$ ). Similarly, fruiting is also significantly negatively correlated to day length and

minimum temperature (Table 4-); note, however, that these environmental variables co-vary.



**Figure 4-5** Monthly percentage of trees with flowers from Transects 1 and 2 with associated rainfall and photoperiod. No data were collected from March 2003 for transect 1.

Over the entire study period of 18 months 211 of 402, or 52.4% of trees that survived the full study period fruited, exactly the same number as those that flowered. This was the same on both transects, with Transect 1 having 52.3% and Transect 2 having 52.6%. Thirty per cent of individuals fruited only once during the study period, while 23% fruited twice. Mean height of fruiting trees was  $19.66 \text{ m} \pm 6.15 \text{ m}$ , while that of trees that did not fruit was  $15.35 \text{ m} \pm 5.35 \text{ m}$ . There was a significant difference between log heights of trees that fruited and those that did not ( $z = 7.555, p < 0.001, n_{fr} = 210, n_{nofr} = 190, z\text{-test}$ ), with fruiting trees being taller. The same relationship is apparent when basal areas are compared, with fruiting trees having larger mean basal areas ( $1102 \pm 1710 \text{ cm}^2$ ) than those that did not fruit ( $340 \pm 348 \text{ cm}^2$ ), as well as significantly larger median basal areas ( $U = 12281, p < 0.001, n_{fr} = 211, n_{nofr} = 191, \text{Mann-Whitney } U\text{-test}$ ).



**Figure 4-6** Monthly percentage of trees with fruits from Transects 1 and 2 including rainfall (mm) and photoperiod. No data from March 2003 for Transect 1.

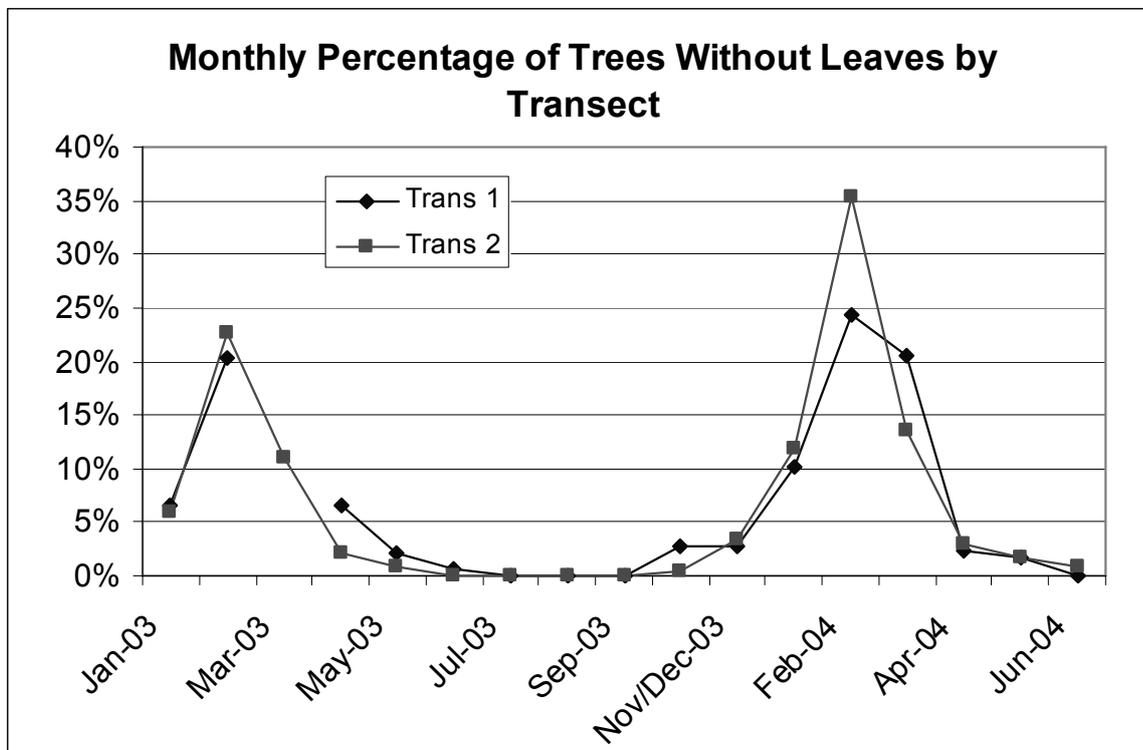
A sample of 33 positively identified species was divided into those that are wind dispersed and those that are not, mainly consisting of fleshy fruits and legumes. In both 2003 and 2004 wind dispersed fruiting peaked in the dry season from December through February, while pulpy fruits showed no clear seasonality, with a bimodal peak in 2003 in April-May and December, with another peak in April through to the end of the study in June 2004. Both fruit types were compared with rainfall, with wind dispersed species found to be negatively correlated ( $r_s = -0.480$ ,  $p = 0.05$ ,  $n = 17$ , Spearman Rank Correlation Coefficient) and non-wind dispersed species not correlating significantly.

### Leaf production cycles

Patterns of leaf loss and leaf flush in the deciduous element of the forest were very similar between Transects 1 and 2. The monthly percentage of transect trees without any leaves is shown in Figure 4-7. This clearly shows that leaf loss occurred dramatically in the early months of the calendar year, notably January, February and March and peaked for both transects in February 2003 and February 2004. In February 2003 both transects had approximately 20% of their trees without leaves, while in February 2004 Transect 1 had 24.5% and Transect 2 had 35%. Considering the entire survey period, there was no

significant difference between transects in frequencies of trees without leaves ( $T = 42$ ,  $p = 0.807$ ,  $n = 13$ , Wilcoxon's test for matched pairs).

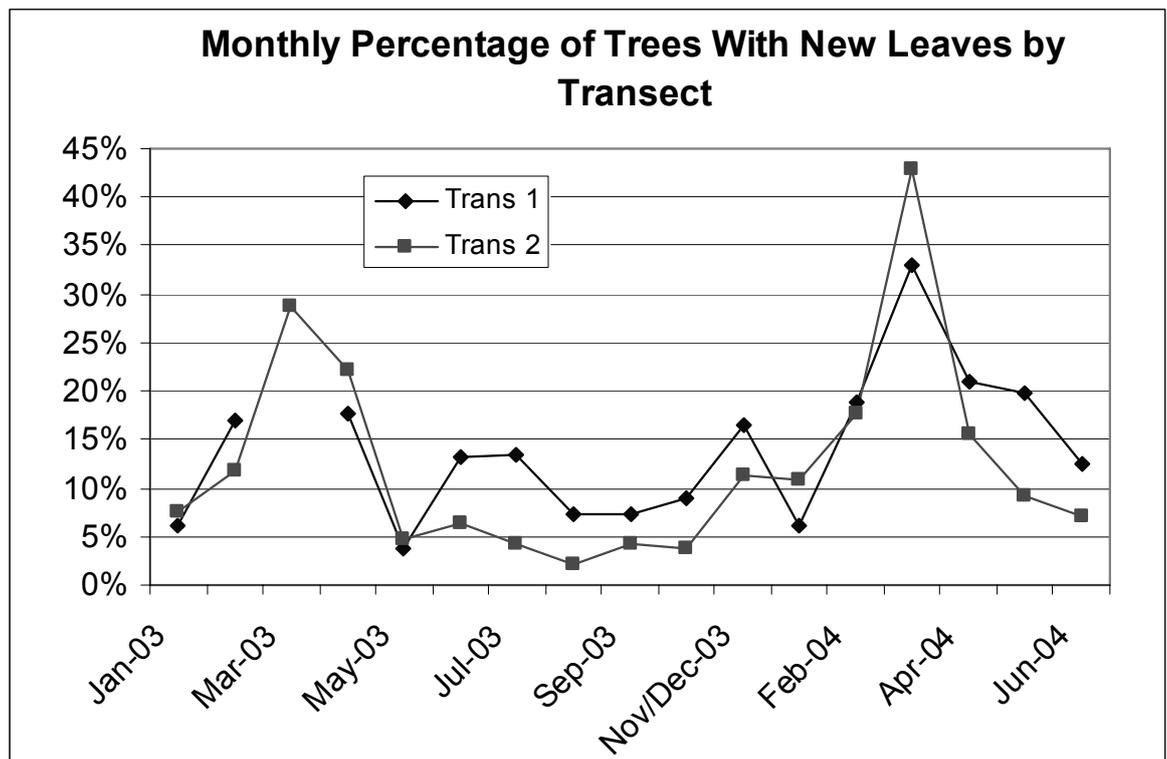
While transects were temporally very similar to each other in patterns of deciduousness, comparisons between years seems to show that for Transect 2, 2004 had a higher percentage of leafless trees than 2003. Comparing frequencies of deciduousness for January to June in Transect 2 (Transect 1 had insufficient data) the differences between years reached significance ( $T = 0$ ,  $p < 0.05$ ,  $n = 6$  months, Wilcoxon's test for matched pairs). It also appears that in some deciduous species patterns were slightly different between 2003 and 2004; for example *Anogeissus acuminata* and *Terminalia* sp. apparently showed delayed leaf abscission in 2003 compared to 2004 (Table 4-2).



**Figure 4-7** Monthly percentage of trees without any leaves from Transects 1 and 2. No data from March 2003 for Transect 1.

Patterns of leaf flush also had distinct peaks in both 2003 and 2004, occurring in March (see Figure 4-8). Frequencies reached 29% for Transect 2 in 2003 with a much higher value of 43% in 2004 and a value of 33% in 2004 for Transect 1. Like patterns in deciduousness, frequency of new leaf flush in 2004 for Transect 2 appeared to be larger than 2003, although median frequencies from January to June in these years are not significantly different ( $T = 5$ ,  $p = 0.25$ ,  $n = 6$  months, Wilcoxon's test for matched

pairs). Similar to temporal patterns in leaf loss, Transect 2 shows a higher peak but tails off much more quickly than Transect 1, with the net result being that frequencies, when averaged out over these peak months, are virtually identical. During the rainy season Transect 1 appears to have higher frequencies of trees with a new leaf flush than Transect 2, but over the full study period differences were not statistically significant ( $U = 104, p = 0.249, n_{\text{tran1}} = 16, n_{\text{tran2}} = 17$ , Mann-Whitney  $U$ -Test).

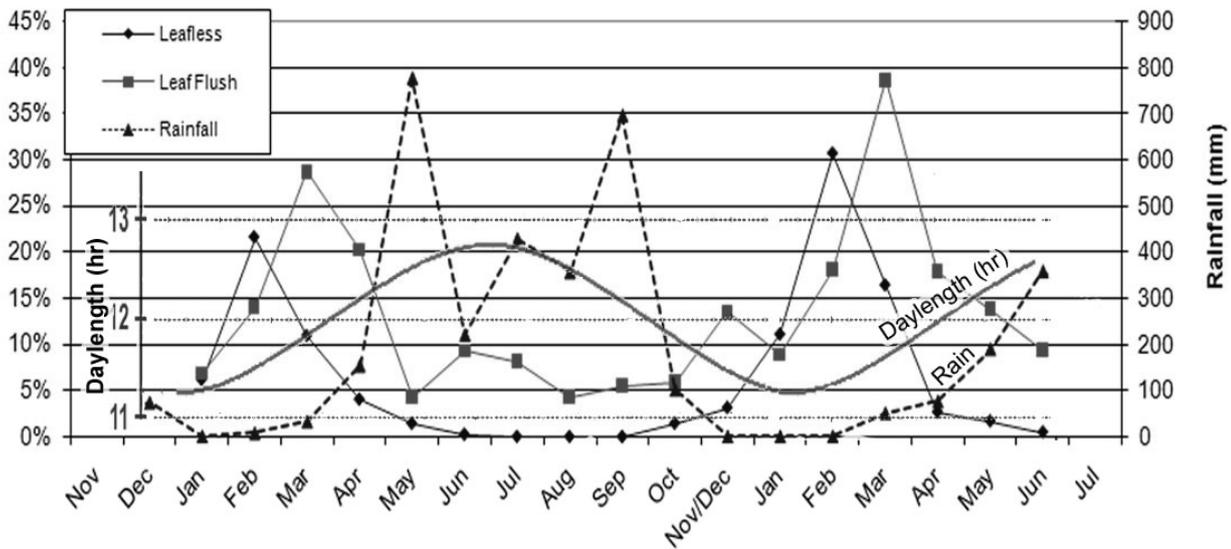


**Figure 4-8** Monthly percentage of trees with new leaves from Transects 1 and 2. No data for March 2003 for Transect 1.

When deciduousness, new leaf flush, rainfall and day length data are plotted together (Figure 4-9), a clear pattern is evident. The deciduous component of the forest sheds its leaves in the months of January through March, peaking in February, inversely correlating significantly with periods of rainfall ( $r_s = -0.842, p < 0.001, n = 17$ ). Leaf loss and rapid subsequent new leaf production are temporally tightly linked ( $r_s = 0.681, p < 0.01, n = 17$ ), with leaf flush peaking in March. This in turn is followed by the start of the wet season proper, but the two events are not significantly correlated. Leaf flush also peaks several months before longest day lengths and the two are not significantly correlated, while frequencies of trees with leaves is significantly related to both periods of greatest rainfall ( $r_s = 0.842, p < 0.001, n = 17$ ) and day length ( $r_s = 0.710, p = 0.001,$

$n = 17$ ). While there is great diversity, both within and between species in leaf phenology, these broad overall patterns of leaf development, maturity and abscission appear to be largely regular between transects and years and can be used to characterise the forest.

**Monthly Percentage of Trees Without Leaves and with New Leaves, Transects Combined**  
and showing rainfall (mm) and daylength (11-13 hours)



**Figure 4-9** Monthly percentage of trees with no leaves and new leaves, transects combined, including rainfall (mm) and photoperiod, November 2002 – August 2004.

Species	<i>n</i>	J	F	M	A	M	J	J	A	S	O	*	J	F	M	A	M	J
<i>A. acuminata</i>	9	Horizontal stripes	Horizontal stripes	Vertical stripes	Flat grey	Flat grey	Flat grey						Horizontal stripes	Vertical stripes	Vertical stripes	Flat grey	Flat grey	Flat grey
<i>L. calyculata</i>	49	Horizontal stripes	Vertical stripes	Flat grey									Horizontal stripes	Vertical stripes	Flat grey			
<i>X. xylocarpa</i>	24	Horizontal stripes	Flat grey	Flat grey	Flat grey								Horizontal stripes	Flat grey	Flat grey	Flat grey		
<i>M. tormentosa</i>	34	Horizontal stripes	Horizontal stripes	Vertical stripes	Flat grey	Flat grey	Flat grey	Flat grey					Horizontal stripes	Vertical stripes	Vertical stripes	Flat grey	Flat grey	Flat grey
<i>Terminalia</i> sp	16	Horizontal stripes	Vertical stripes	Flat grey									Horizontal stripes	Vertical stripes	Vertical stripes	Flat grey		

**Table 4-2** Simplified phenological patterns in leaf loss and flush for some deciduous or largely deciduous dominant species, January 2003 – June 2004.

\* November and December                      Horizontal stripes = shedding  
Vertical stripes = leafless                      Flat grey = new leaf flush

Note: Phenology data for March 2003 all come from Transect 2.

		Fruit	New Leaf	Decid †	Rainfall	Day Length	Min Temp	Max Temp
<b>Flower</b>	Correlation Coefficient	.056	<b>.735(**)</b>	<b>.543(*)</b>	-.390	-.092	-.349	.407
	Sig.(2-tailed)	.791	<b>.001</b>	<b>.024</b>	.122	.725	.169	.105
	<i>n</i>	17	<b>17</b>	<b>17</b>	17	17	17	17
<b>Fruit</b>	Correlation Coefficient		-.196	.376	<b>-.587(*)</b>	<b>-.804(**)</b>	<b>-.716(**)</b>	<b>-.520(*)</b>
	Sig.(2-tailed)		.451	.137	<b>.013</b>	<b>.000</b>	<b>.001</b>	<b>.033</b>
	<i>n</i>		17	17	<b>17</b>	<b>17</b>	<b>17</b>	<b>17</b>
<b>New Leaf</b>	Correlation Coefficient			<b>.681(**)</b>	<b>-.488(*)</b>	-.155	-.314	<b>.608(**)</b>
	Sig.(2-tailed)			<b>.003</b>	<b>.047</b>	.553	.220	<b>.010</b>
	<i>n</i>			<b>17</b>	<b>17</b>	17	17	<b>17</b>
<b>Deciduous †</b>	Correlation Coefficient				<b>-.842(**)</b>	<b>-.710(**)</b>	<b>-.703(**)</b>	.396
	Sig.(2-tailed)				<b>.000</b>	<b>.001</b>	<b>.002</b>	.116
	<i>n</i>				<b>17</b>	<b>17</b>	<b>17</b>	17

**Table 4-3** Spearman Rank Correlation Coefficient matrix for phenophases and environmental variables. Significant values are in bold type.

\*\* Correlation is significant at the 0.01 level (2-tailed).

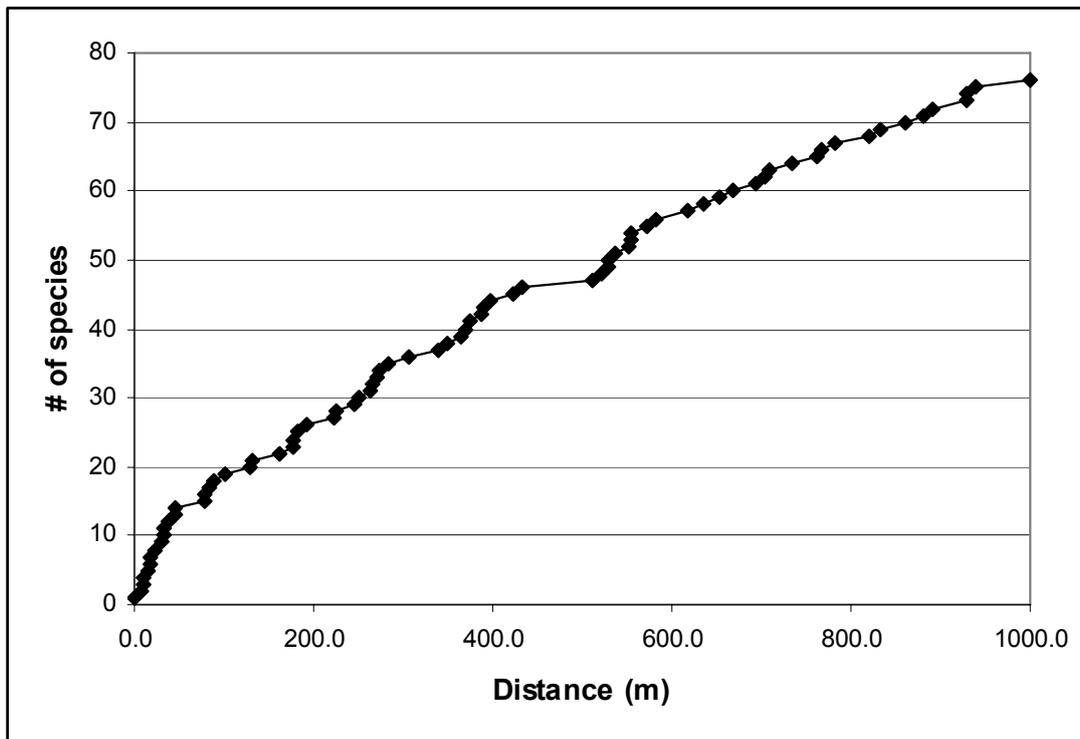
\* Correlation is significant at the 0.05 level (2-tailed).

† Same value but inverse sign for trees with leaves.

### *Species richness and diversity*

Of the 429 plants  $\geq 10$  cm DBH on Transects 1 and 2, a total of 348 were identified to at least the level of family. This included 66 species belonging to 57 genera and 34 families positively identified from Transects 1 and 2, an area which constitutes approximately 1 hectare. Appendix one lists all taxa identified. A total of 81 trees, or 23%, remained unidentified at the end of the study. Some of these were apparently of the same species, but definite distinction was difficult.

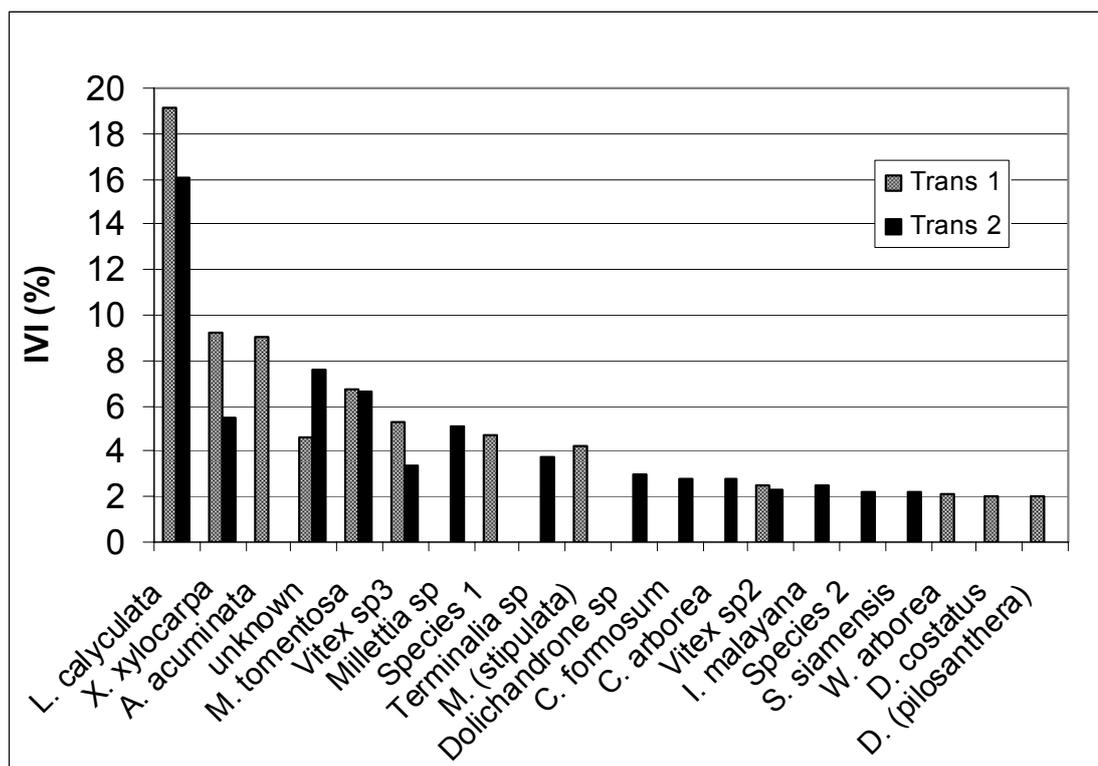
The incidence of new species by distance down transects was plotted to determine whether transects had captured a significant proportion of the botanical diversity at the site (Figure 4-10). Though new species were still being recorded in the last 100 m many



**Figure 4-10** Species incidence curve for Transects 1 and 2 combined.

species in the habitat were captured by transects. The limitation of having a relatively low percentage of transect trees precisely identified, however, makes problematic the determination of exactly what proportion of species were captured.

Importance Value Indices (IVI) were calculated for all species by transect, with results presented in Figure 4-11. In this index, the higher the value, the more dominant the tree species is in the environment. It can be seen that *Lagerstroemia cf. calyculata* was the most dominant taxon at the site, with over 15% of IVI values on both transects. *Xylia xylocarpa* was the next most dominant tree species, occurring on both transects, followed by *Microcos tormentosa*. *Anogeissus acuminata* also returned high IVI values, but only occurred on Transect 1. Transects did not have statistically different IVI rank orders for the top 20 tree species ( $r_s = 0.161$ ,  $p = 0.449$ ,  $n = 20$ ).



**Figure 4-11** Percentage of Importance Value Index (IVI) for dominant plant species (IVI  $\geq$  2.0) by transect.

## Discussion

### *Forest structure*

Analysis of variance in tree size showed that the stratigraphy of Transect 3 was significantly different from either Transect 1 or two, having an average upper canopy layer several metres shorter. Its high relative frequency of stems in lower DBH sizes, and large number of stems/ha, is contextualised well by comparisons with work from Cat Tien National Park, where similar numbers for these variables were reached only in very disturbed areas (Blanc *et al.*, 2000's plot C). This all suggests that this area was very disturbed at some point in the past and is now undergoing regeneration. Because of this, Transect 3 was not utilised for phenological monitoring or species identification, as the study aims did not include a comparison of relatively undisturbed and disturbed habitat types.

While no comparable data from elsewhere in Cambodia were available for tree heights, figures for tree basal area/ha from the three transects are comparable to figures derived from a tree species composition study, conducted in SBCA (Zimmermann and

Clements, 2002). That study collected data from six 1000 m x 10 m transects, a total of 6 ha, across gradients in semi-evergreen/mixed deciduous forest from coupes 3 and 5, some of which were very close to the study site. Average basal area from these transects was  $31.1 \pm 4.7 \text{ m}^2/\text{ha}$ , although only trees  $\geq 19.11 \text{ cm DBH}$  were included, unlike this study which used a figure of  $\geq 10 \text{ cm DBH}$ . When basal area from the current study is calculated using only trees  $\geq 19.11 \text{ cm DBH}$ , the figure from all transects combined is  $28.9 \pm 3.8 \text{ m}^2/\text{ha}$ . This slightly lower value than that of Zimmerman and Clements (2002) is most likely because, while four of their transects crossed semi-evergreen/mixed deciduous gradations similar to the study site, the other two transects were in largely undisturbed evergreen forest, probably increasing the average.

Other areas of Cambodia from which data are available include two sites located c. 130 km from the study area, situated between Krek and Mimot. Rollet (1972, in Rundel, 1999) gave details of a *Lagerstroemia* dominated forest here with densities of 338 and 256 trees/ha for trees  $\geq 10 \text{ cm DBH}$ , but gave no basal areas. Hozumi (1969, in Rundel, 1999) gave density estimates for wet evergreen forest in the Cardamom Mountains in south-west Cambodia as 356-412 trees/ha with  $\text{DBH} \geq 10 \text{ cm DBH}$  and an estimated basal area of  $31.9 \text{ m}^2/\text{ha}$ , similar to figures presented here.

With floristic studies in Cambodia being in their infancy, adjacent similar forest types in Vietnam provide one of the few other data sources for comparison with the study site. Best described of these is Cat Tien National Park, which is located approximately 100 km east of the study site and contains a very similar species composition, although is probably more disturbed. Five 1 ha plots in the western lowlands of the park returned basal area values of (A)  $69.41 \text{ m}^2/\text{ha}$ , (B)  $31.71 \text{ m}^2/\text{ha}$ , (C)  $54.89 \text{ m}^2/\text{ha}$ , (D)  $29.30 \text{ m}^2/\text{ha}$ , and (E)  $31.33 \text{ m}^2/\text{ha}$  (Blanc *et al.*, 2000). While plots B, D and E are comparable to the study site, plots A and C are clearly far in excess of those found in this study. These large basal areas were explained in the case of plot A by the dominance of large *Lagerstroemia calyculata* trees, suggestive of secondary forest about to undergo species transition, and in the case of plot C by the large number of smaller diameter trees, suggestive of an area undergoing regeneration (Blanc *et al.*, 2000). Plots B and E were assessed by them to be representative of mature forest, based partially on DBH size classes, the distribution of which matches well with those from this study, having tree densities of 389 and 469 trees/ha respectively. Together, this

evidence suggests that the forest at the study site is probably also representative of mature forest.

Location	Minimum DBH (cm)	Basal Area (m <sup>2</sup> /ha)	Stem Density (stems/ha)	Reference
Mondulkiri, Cambodia	19.11	31.1	212	(Zimmermann and Clements, 2002)
Kampong Cham, Cambodia	10		338, 256	(Rollet, 1972)
Cardamoms, Cambodia	10	31.9	256-412	(Hozumi <i>et al.</i> , 1969)
Cat Tien NP, Vietnam	10	31.71, 31.33*	389, 469	(Blanc <i>et al.</i> , 2000)
Transect 1	10	28.0	350	This study
Transect 2	10	33.5	444	This study
Transect 3	10	32.7	507	This study

**Table 4-4** Summary of forest structural data from other studies compared to this study.  
\*Plots representing mature forest in Cat Tien NP.

The levels of mortality found during this study were comparable to studies in other regions. The rate of tree mortality at the site, 1.55% of all trees/year, was within the range of other published figures (see Lewis *et al.*, 2004 for a comprehensive review) and comparable to Lewis *et al.*'s (2004) pan-tropical average turnover rate of 1.81% of all trees/year. The presence of dead and dying trees has been noted to be a good indicator of forest health as they provide habitats for animals (McDonald, 2003). The cause of death was not determined for any trees during the study, but the deaths were spatially and temporally distributed with no indication of disease. In August 2003, a large section of understory was anthropogenically burnt towards the end of Transect 2, but this had not resulted in any tree mortality by the end of the study.

In short, the structure of the forest seems comparable with other areas in Cambodia and the region and seems to be representative of relatively undisturbed mature forest.

## ***Phenological patterns at the site***

### **Flower production**

Monthly production of flowers was quite variable at the study site, with a range of about 1% - 16% of all transect trees having flowers. This variability fits well with other studies from Southeast Asia which generally range from only a few percent of trees flowering in any month to a maximum of about 20% (e.g. Raemaekers *et al.*, 1980, Boonratana, 1993, Bartlett, 1999). These levels of flowering at the site may be an underestimate, however, as it is probable that some flowering events were missed due to short periods of flower persistence in some species coupled with only once-monthly phenology walks. Flowering tended to peak during the dry season just before the rains, after which frequencies dropped off markedly. Extensive flowering during the dry season is not uncommon for other seasonally dry tropical forests sites (e.g. Frankie *et al.*, 1974, van Schaik *et al.*, 1993, Murali and Sukumar, 1994, Bartlett, 1999) although variability is great and many show a bimodal pattern in production, which was not strongly evidenced here.

Only about half of all trees flowered during the study period. Of course not all trees would be expected to flower as many of the smaller trees would not yet be fertile (Wright *et al.*, 2005) and some trees don't flower every year even if mature (Frankie *et al.*, 1974). The fact that smaller trees were less likely to be fertile was demonstrated by the finding that trees that flowered were found to be significantly taller and to have larger basal areas than those that did not. In terms of flowering consistency across years, only about half of the flowering trees actually flowered twice during the study, while the other half flowered just once. This suggests that not all fertile individuals flowered annually at the site, although it is presumed that the percentage of trees flowering twice would have increased had the length of study been increased to two years, despite the fact that the second half of 2003 showed low levels of flowering which would have presumably been similar in 2004.

Although many environmental cues have been identified or can be hypothesised to cause flowering in tropical plants, such as colder temperatures (Whitmore, 1984), changing photoperiod (Leopold, 1951), rainfall (Opler *et al.*, 1976) and increased radiance (Wright and van Schaik, 1994), none were clearly shown to be factors affecting flowering at the site. This may not be that surprising, as different species respond to different cues, resulting in a diverse range of simultaneous phenologies.

Further confounding environmental cues, flower development in trees may show a delay of months between flower induction and anthesis (Borchert, 1983), the point at which flowering will be noted during phenology walks.

Flowering was however significantly correlated with deciduousness and new leaf production, phenomena which are quite tightly synchronised around the beginning of the calendar year at the site. During this time the deciduous element of the forest loses its leaves which are then replaced by new growth, leaving a very open canopy for several months. It has been argued that flowering during periods of leaflessness may be a strategy to improve pollination. Van Schaik *et al.* (1993) suggested that plants whose pollen is wind-dispersed would do best to flower when there were few leaves in the canopy to obstruct the passage of pollen grains. Murali and Sukumar (1994) suggested that flowering at this time would be beneficial for animal pollinated plants also, as flowers would be easier to see. Unfortunately neither of these hypotheses can be tested from data generated during this study as windiness was monitored only in the morning in relation to gibbon vocalisations (Rawson, 2004), with mornings being invariably calm.

### **Fruit production**

Levels of fruit production from the transects were quite variable between months but averaged around 13%. These levels seem quite high when compared with studies in other regions. For example, Chapman *et al.* (2005) found average monthly levels of only 3.97% over 30 years at four sites in Kibale National Park, Uganda, while Palombit's (1992) site in Sumatra averaged  $7.7\% \pm 4.3$ , and Bartlett (1999) quotes a maximum of 9% from Khao Yai National Park, Thailand. Likewise, the percentage of trees fruiting over the 18 months of the study was high at 52.5%, compared to figures of yearly total of 37% in Sumatra (Palombit, 1992), and 18% in the Malay Peninsula (Raemaekers *et al.*, 1980) but similar to the Dipterocarp dominated forests of Sarawak, Malaysia with 45.73% (Gumal, 2001). As with flowering, trees with larger basal areas and heights were found to be more likely to fruit.

Temporal patterns in fruiting at the site demonstrated clear seasonality, with higher levels of fruiting being correlated with drier periods of the year. The relationship between rainfall and fruiting is not clear, although one comprehensive review suggested that in many areas fruiting is concentrated at the start of the wet season in seasonally dry forests, to avoid seedling mortality in the dry season (van Schaik *et al.*, 1993). While

this contradicts the results found here, patterns of fruit production may be obfuscated as different fruit types with different modes of dispersal and different predation pressures may be optimally adapted to fruit at different times of the year. For example, wind dispersed species may fruit in the windiest time of the year while those that are susceptible to seed predation may drop fruit at the start of the wet season to reduce the amount of time spent on the forest floor (van Schaik *et al.*, 1993).

Differential modes of dispersal may be masking temporal fruiting patterns in relation to rainfall at the site. Wind-dispersed fruits correlated negatively with rainfall while other fruit types did not suggesting that this may be partially the case. Without data on windiness it is difficult to say whether this was the ultimate reason for this pattern; dry season maturation of dry fruits has been noted elsewhere (Lieberman, 1982). There was no trend towards fleshy fruit maturation during the wet season contrary to many other studies (e.g. Lieberman, 1982, van Schaik *et al.*, 1993, Murali and Sukumar, 1994), but when wind dispersed fruits are removed from analysis it clarifies that fleshy fruits are not necessarily prone to mature during dry periods as might otherwise be inferred. Instead, fleshy fruit production showed bimodality; the first peak in May-April 2003 and 2004 coincided with the first period of very heavy rains, while the second in December coincided with the start of the driest time of year. We must recognise, however, that fruiting may not be timed only for optimal dispersal but it may also be limited by the availability of resources in the preceding months (Tutin and Fernandez, 1993, Chapman *et al.*, 2005).

General patterns of fruiting at the site are likely therefore to be caused by a dynamic interplay between current and past environmental conditions and adaptations for dispersal and predator avoidance, too complex to unravel using the limited data and relatively simple analyses presented here.

### **Leaf production**

Patterns of leaf abscission and new leaf flush at the site showed a clear pattern for both 2003 and 2004, with trees losing their leaves towards the end of the dry season, quickly followed by new leaf production before the first rains. It is generally accepted that leaf abscission, while widely variable in calendar timing and in duration of the leafless period, both between species and within species between years, is largely related to environmental water availability or water stresses (Borchert *et al.*, 2002). It is therefore reasonable to assume that leaf loss occurs at the site in response to reduced moisture

during the prolonged dry season. Leaf loss would also reduce water loss otherwise occurring through transpiration.

This being the case, it is paradoxical that new leaf flush occurs before the first rains of the monsoon, as one would expect that this would not only place additional water stress on the tree through increased transpiration, but that trees would not be capable of expanding this new foliage because of their water deficits. Rainfall events of >30 mm may be required to trigger a new leaf flush (Borchert, 1994a), yet at the site rainfall was well below this critical level when leaf flush began, especially in 2003 when the first rain of this magnitude was on April 24<sup>th</sup>, four to eight weeks after most individuals had undergone leaf flush. Research in the field of leaf phenology in seasonally dry tropical forests, however, shows that this is often the case in these environments, from India to Thailand to Costa Rica (Borchert, 1994b, Rivera *et al.*, 2002, Kushwaha and Singh, 2005, Elliot *et al.*, In Review). This pre-monsoonal leaf flush is apparently species-specific (Rivera *et al.*, 2002), and has resulted in the moniker ‘spring-flush’ species.

This behaviour, as shown at this site and others, is apparently cued independent of rainfall; it has been theorised to be triggered instead by increasing photoperiod as the spring equinox approaches (Rivera *et al.*, 2002). The rationale is that increasing day length is an indicator of the coming monsoon, and new leaf flush can be initiated on this environmental cue in pre-emption of the rains. When the rains do arrive, the tree already has photosynthetically efficient leaves but has not exposed itself unduly to transpiration during the dry season, effectively extending the relatively short wet growing season (Rivera *et al.*, 2002, Kushwaha and Singh, 2005, Elliot *et al.*, In Review). This makes sense, as newly expanded leaves are better able to control transpiration and are more efficient at photosynthesis (van Schaik *et al.*, 1993). Increasing photoperiod matches well with new leaf flush at the site.

Both of these factors, control of transpiration and having photosynthetically efficient leaves, may be important in the early wet season at the site to mitigate against patchy rainfall and to take advantage of the year’s first solar zenith, which occurs at the site on 23<sup>rd</sup> April (MIDC). Solar radiation is considerably higher when the sun is at the zenith and, not surprisingly, maxima in leaf and flower flush are proximally related to this time in many forests (van Schaik *et al.*, 1993, Wright and van Schaik, 1994). At the study site the sun’s angle peaks in April and then again in August, with the intervening period having similarly high levels as well as the longest day lengths (June-July), resulting in

peak levels of daily irradiance. Spring-flush would therefore seem to be timed to take maximum advantage of the start of these high levels of irradiance, with trees subsequently having a full complement of leaves throughout this period of high irradiance to maximise carbon fixation and growth.

New leaf flush at the end of the dry season also requires a source of moisture in order to begin new leaf production, but the variables associated with moisture availability and access are many, including root depth (van Schaik *et al.*, 1993, Sayer and Newbery, 2003), soil structure (Kusar *et al.*, 2005) and stem water storage ability (Borchert, 1994a). The fact that a large proportion of trees at the study site undergo “spring-flush” suggests that subsoil moisture is likely available to these individuals in this later section of the dry season but further discussion is beyond the scope of this thesis.

One line of evidence does suggest however that leaf abscission is related to water stress and not temporally tuned to other environmental variables. The variability in leaf fall on Transect 2, with trees in 2004 showing higher frequencies of deciduousness than in 2003 (data not shown), may possibly be connected with significant rainfalls during one week in late November/early December 2003, when 60 mm of unseasonable rainfall was recorded. This rain, along with a quicker onset of the monsoon (relative to 2004), may have been responsible for lower levels of complete leaf exchange in Transect 2 in 2003.

This is hinted at also by the phenological behaviour of the wholly deciduous species *Anogeissus acuminata* and *Terminalia* sp. which showed delayed leaf abscission in 2003, not becoming wholly leafless until March for the former and February for the latter, which is one month later than for 2004 for both species). This pattern was not noticeable in any other of the dominant deciduous species however and did not change the timing of new leaf production.

### ***Habitat typologies: when is semi-evergreen mixed deciduous?***

Classifying the habitat of the study site is difficult primarily because there is no generally recognised framework for the Central Indochina Dry Forests. Classification of habitats in Cambodia poses a particular problem as botanical fieldwork and publications are very limited. Some comparisons are possible with southern Vietnam, but the majority of Vietnamese forests are qualitatively different to those of Cambodia. Thailand once possessed extensive dry forests similar to those in Cambodia but much

has been converted to agriculture. This leaves little comparative information for work in Cambodia. The individual study site poses more problems, being located in an ecotone between the Indochinese Dry Forests and the evergreen dominated forests of the southern Annamite Mountains.

Generally, workers in Cambodia have divided habitats along a gradient of deciduousness, from evergreen forest through semi-evergreen forest, mixed or nearly deciduous forest, to dry deciduous or dry deciduous dipterocarp forests (Timmins and Men Soriyun, 1998, Long *et al.*, 2000, e.g. Timmins and Ou Rattanak, 2001, Walston *et al.*, 2001). While these provide general outlines for comparison between areas, they are problematic as the location of each point along the gradient is not specified. Furthermore these terminologies are reliant on the observers' subjective evaluation of them, which is in turn reliant on the breadth of the observer's previous experience, leaving the way open to inter-observer inconsistency (Zimmermann and Clements, 2002).

Of particular relevance for the study site is the distinction, if indeed one exists, between semi-evergreen and mixed deciduous forest types (Walston *et al.*, 2001, Maxwell, 2003), the two major forest "types" commonly used to describe the study site area. Rundel (1999) distinguished between these two forest types using the following general criteria:

- Mixed deciduous has a canopy of c.30 m with few lianas and epiphytes; understorey is open but diverse; there is a leafless period of four to five months; dominant and co-dominant species include Fabaceae (*Xylia kerrii*, *Pterocarpus macrocarpus*, *Dalbergia* spp.), Combretaceae (*Terminalia* spp.) and Lythraceae (*Lagerstroemia* spp); Dipterocarps largely absent except in transition to deciduous dipterocarp.
- Semi-evergreen has a slightly higher canopy of 30-40 m in which lianas may be common; the understorey is not overly diverse and may have significant amounts of bamboo in disturbed areas; rainfall is generally in the region of 1200-2000 mm with a three to six month dry period when a significant proportion of trees lose leaves; species richness is quite low relative to evergreen forest with low levels of dipterocarps except in transitional areas into deciduous dipterocarp forest. Because of their diversity, species composition is not a useful tool for categorising this forest type; an example of species in a "typical" semi-evergreen forest might have

emergents that are predominantly dipterocarps (e.g. *Dipterocarpus alatus*, *D. costatus*, *Hopea odorata*, *Ficus* sp., *Tetrameles nudiflora*) with a canopy composed of species such as *Lagerstroemia* sp., *Irvingia malayana*, *Adina cordifolia*, *Wrightia* sp., *Alstonia* sp., *Diospyros* sp. with a diversity of legumes such as *Sindora siamensis*, *Pterocarpus macrocarpus*, and *Afzelia xylocarpa*.

While laying down these broad identification schemes, Rundel (1999) accepted that differentiating between what he saw as two distinct habitat types is problematic, as in reality they may intergrade into one another. He argued however that the forests of northern Cambodia, which include the study site, should be classified as semi-evergreen, not mixed deciduous as they often have been, and that this mistaken identification is because they actually represent a quite unique deciduous type of semi-evergreen forest.

Zimmerman and Clements (2002), working very close to the study site, attempted to clear up these typological problems by looking at gradients in species composition between habitat types. They found that no discreet habitat types could be identified along their transects between gallery semi-evergreen forest through to deciduous dipterocarp forest. Instead species composition changed in a gradational way between these habitat types, the relative dominance of particular species along this axis possibly related to moisture availability, although other factors were hypothetically implicated. Despite this blurring of forest types, they did find, contrary to Rundel's (1999) suggestion, that the dominance of certain species could be used as indicators or broad definers of these habitat types.

Based on data presented here, Rundel's (1999) broad classifications, and the work at the site of Zimmerman and Clements (2002), it is clear that the site is a mixture of semi-evergreen forest and mixed deciduous forest, with representatives of both habitat types present on both phenology transects. Transects clearly sampled both of these habitat types, although based on IVI values presented in Figure 4-11, it appears that Transect 1 falls closer to the mixed deciduous end of the spectrum, while Transect 2 conforms more to the species composition expected from semi-evergreen forest types. Ultimately, the site is largely a mosaic of these two forest types. The approach and terminology used throughout this study to distinguish these habitat types uses the relative abundance of *Lagerstroemia cf. calyculata* as a guide, with areas where this species clearly

dominates being classified as mixed deciduous forest. This appears to be the cleanest way to cut the Gordian knot of these enmeshed habitat typologies.

## Summary

The study site is located in relatively undisturbed forests best described as a mosaic of semi-evergreen and mixed deciduous forest types. The forest was species-rich and characterised by the family Dipterocarpaceae and by Legume species and dominated by *Lagerstroemia cf. calyculata*, *Xylia xylocarpa*, and *Anogeissus acuminata*. The canopy is approximately 20 m high through most of the area, with emergents reaching a maximum of 40 m. Basal area/ha and tree stem density/ha are comparable to other sites in the immediate region and southeast Asia in general. Understorey is variable, apparently dependent to some degree on tree species composition, stem density and disturbance.

It appears that distinct wet and dry seasons dictated phenological cycles, with the deciduous component of the forest losing its leaves at the tail-end of the dry season from January to March, followed immediately by new leaf flush just prior to the beginning of the wet season. Flowering patterns, while not as marked as those for leaves, and reflecting the large number of species flowering independently in the forests, showed a peak just prior to new leaf flush, continuing on for some months, with low overall levels of production during the wettest months of the year. Fruit production showed no clear temporal patterns.



## ***Activity budgets and behaviour***

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### **Introduction**

Little information exists on the behaviour and activity budgets of the genus *Pygathrix* in the wild. The first data came from important preliminary studies in Vietnam on *P. nemaesus* (Lippold, 1977, Lippold, 1998), while more recently, data on activity budgets in black-shanked doucs have become available (Rawson, 2006, Hoang Minh Duc, 2007). Studies on the genus in captivity are more readily available, and provide a baseline of information for comparison of behaviours observed during this study. All captive studies to date concern *P. nemaesus*, the majority of these from studies performed during the 1970s and 80s at zoos at San Diego (Hill, 1972, Kavanagh, 1972, Brockman and Lippold, 1975, Kavanagh, 1978, Lippold, 1981) and Cologne (Hollihn, 1973, Ruempler, 1998). More recently, some research has emerged from the Endangered Primate Rescue Center (EPRC) in Vietnam. The most relevant of this for comparison here is the work of Otto (2005), who looked briefly at activity budgets in captive and semi-free ranging animals. Other work from the EPRC has tended to focus on locomotion (Byron and Covert, 2004, Covert *et al.*, 2004, Workman and Covert, 2005), which provides a good basis for comparison with data from this study.

This chapter represents an attempt to typify the behaviour of *P. nigripes*. While data quality is low in some instances due to the frailties of observational studies on arboreal, rainforest primates, the general themes are clear and provide a solid basis for additional studies and comparison across the subfamily Colobinae.

### **Methods**

Data on *P. nigripes* activity patterns were collected between April 2003 and August 2004. Because the animals were never habituated, and because of my initial inexperience in observing animals without disturbing natural behaviours, data acquisition in the early months was minimal and sporadic. This has implications for analysis across the study period as many behaviours were not recorded in this original period due to lack of observation time. Furthermore, there are several months where data were insufficient for comparison, resulting in seasonal as opposed to monthly comparisons.

Data were collected in an *ad hoc* manner, with no strict rotation between age and sex classes to ensure equal representation, as this was usually not possible due to viewing conditions. General rules for selecting an individual for observation (although see Chapter 3 for more detail) were: the first animal seen became the focal animal and remained so until it was no longer in sight; dependent infants were excluded unless no other individual was available for observation (infant data are not included in analysis here unless stated otherwise). Despite this, male ( $n = 1421$ ) and female ( $n = 1380$ ) data sets are similar in size, though immatures (subadults and juveniles lumped to increase data set size) are under represented ( $n = 645$ ).

A focal animal instantaneous sampling protocol with a 30 second interval was used for reasons discussed in Chapter 3, resulting in 4476 samples across 295 encounters made over c.297 field days (some days were not dedicated to primate survey work.) Five non-overlapping behavioural categories were used, each with its own subcategories based on a short pilot study. See Chapter 3 for a full ethogram with definitions of each activity category.

One-way chi-square tests were performed on inter-hour and age/sex class variation in daily activity pattern data, one each for each major activity type; the significance level was set at  $p < 0.01$  in both instances because multiple tests were performed. One-way chi-square tests were also used to determine if foods consumed varied by age/sex class, if activities in general and scanning in particular occurred differentially in different canopy layers, whether grooming was randomly distributed between dyads, and whether timing of births was non-random. For these tests significance levels were set at  $p < 0.05$ .

Tests for correlation between major activity categories of ‘inactive’, ‘feed’ and ‘travel’ were performed using Spearman Rank Correlation Coefficients, while the Mann-Whitney *U*-test was used to detect seasonality in major activity categories, and in diet with significance levels set at  $p < 0.01$  in both instances as multiple tests were performed.

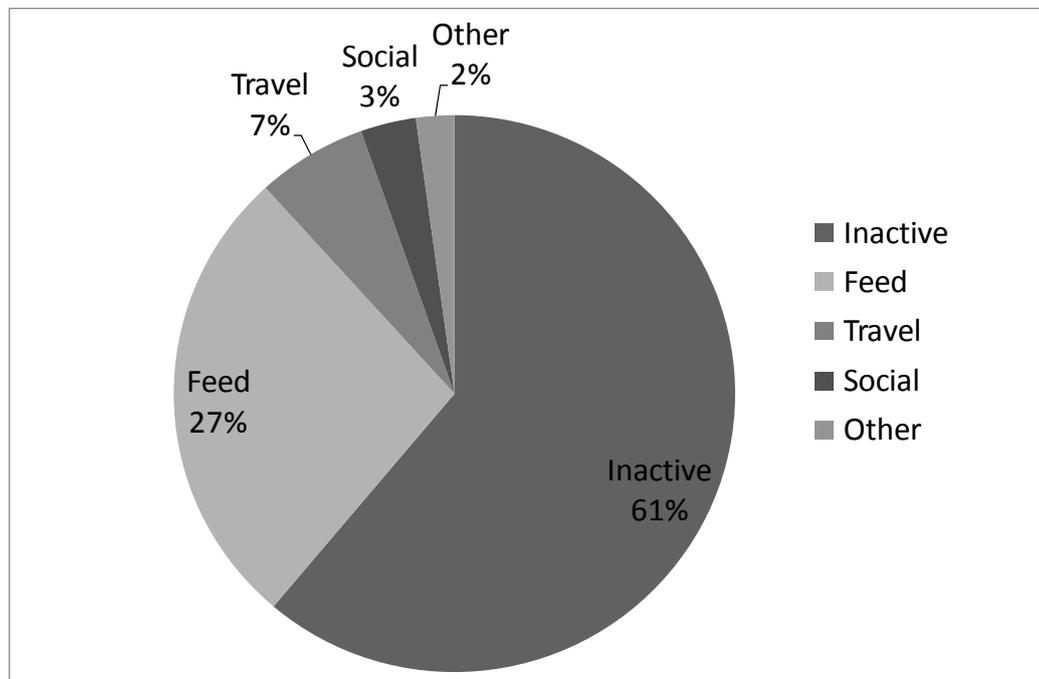
All statistical tests were performed using SPSS 11.5.

## Results

### *Activity budget*

Within the highest level of activity categories, behaviours were divided into five non-overlapping types: inactive, feeding, travelling, social behaviours and other activities. This study looks first at the patterns for the species as a group, with both sexes and all ages (except infants) lumped, giving  $n = 4443$ . Results show that inactivity dominated with a frequency of 61%. Feeding occupied 27%, travelling 7%, social behaviour 3% and other activities 2% (see Figure 5-1).

Tests for correlation between major activity categories showed a negative correlation between 'inactive' and 'feed' categories ( $r_s = -0.971$ ,  $p < 0.01$ ,  $n = 11$ ) but no other significant values were obtained.



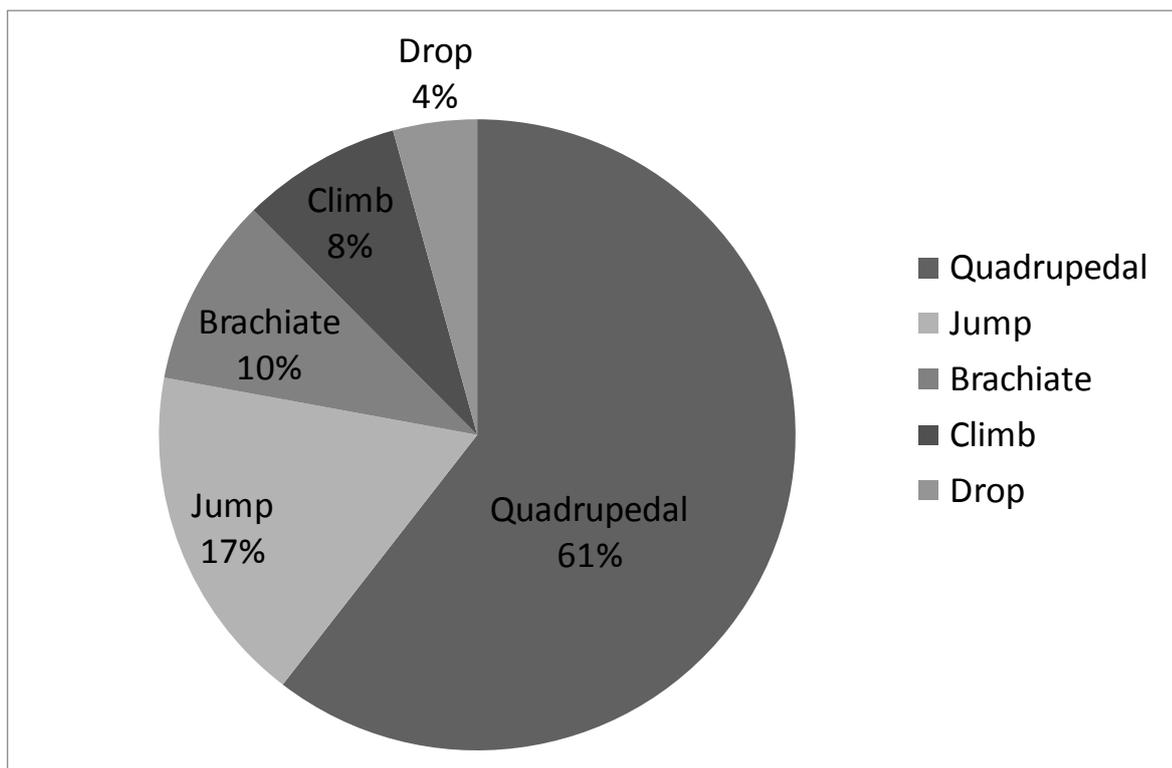
**Figure 5-1** *P. nigripes* activity budget. Age and sex classes lumped, excluding infants ( $n = 4443$ ).

### *Category subdivisions*

Each of the major categories was comprised of several sub categories. To give a quick overview figures for the subdivisions of locomotion and social activities are given in pie charts in Figures 5-2 and 5-3 and Table 5-1. Feeding behaviour was divided into the consumption of eight different food types; a comprehensive assessment of feeding ecology is not presented here but rather given in Chapter 7.

Inactive behaviours, which made up the largest contribution to the total activity budget, contained two sub-categories: inactive and scanning. Inactive dominated with 94.2% with scanning behaviour making up the remainder at 5.8%.

Travel was divided into five sub-categories. Quadrupedal travel dominated locomotive behaviour, comprising 60.5% of observations. Jump at 17.4% was next, followed by lower levels in decreasing frequency of brachiate 9.7%, climb 8.1% and drop 4.3% as shown in Figure 5-2.

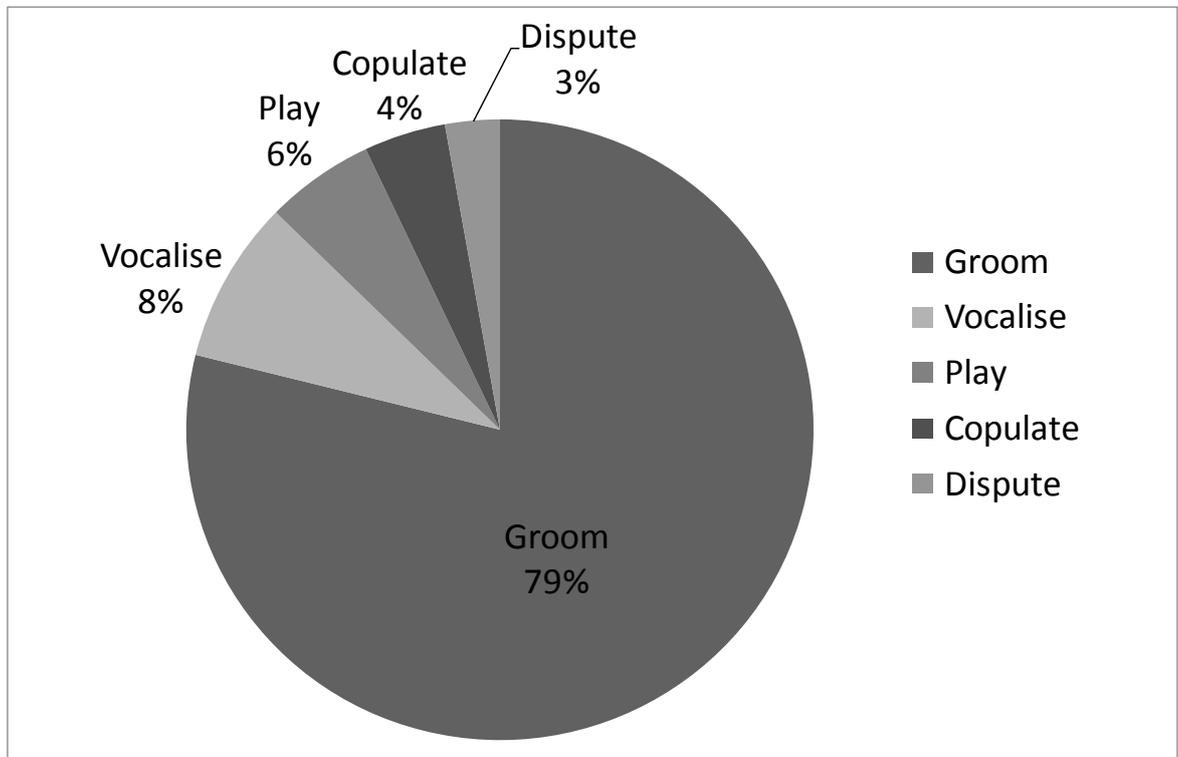


**Figure 5-2** Frequencies for travel using different locomotion types, age and sex classes lumped excluding infants ( $n = 258$ ).

All categories noted under social behaviour except for grooming have very small sample sizes. These sampled frequencies (see Figure 5-3) are therefore unlikely to approximate actual values for these behaviours to any significant degree and should be interpreted with caution.

Grooming dominated the social activity budget, comprising 78.9% of all samples. Unreciprocated grooming behaviour was noted between adult females and infants, while reciprocated grooming was observed between adult females and adult males, subadult females and adult males, and juveniles of unknown sex and males.

Vocalisations were rarely noted during sampling, comprising only 11 observations, some of which may have been in response to the observer. All instances come from males, and were either contact calls or alarm calls. Females were heard to vocalise occasionally outside of sampling, generally in response to male contact calls.



**Figure 5-3** Frequencies for social behaviours, age and sex classes lumped, excluding infants ( $n = 153$ ).

While infants frequently exhibit play behaviour, other age classes are seldom involved in play behaviour. Play behaviour entered into by adult or subadult individuals was represented by only eight observations during the study. Behaviours interpreted as play were quite variable: two instances being of males playing intently with their own feet, one of a female subadult grabbing a juvenile's tail that was hanging in front of her, and a few of adults and subadults playing briefly with infants when harassed.

Copulation was observed only once and is described in detail in the Copulation section below. Disputes were very rare and instances are described in the Agonistic behaviours section below.

Other activities comprised a very small percentage of the overall activity budget. By far the most common activity in this category was the autogroom behaviour, which

comprised 95% of observations. This was followed by defecate and urinate with 3% and 2% respectively. Nursing was a category also included in other behaviours but is excluded here as only adult females performed this behaviour.

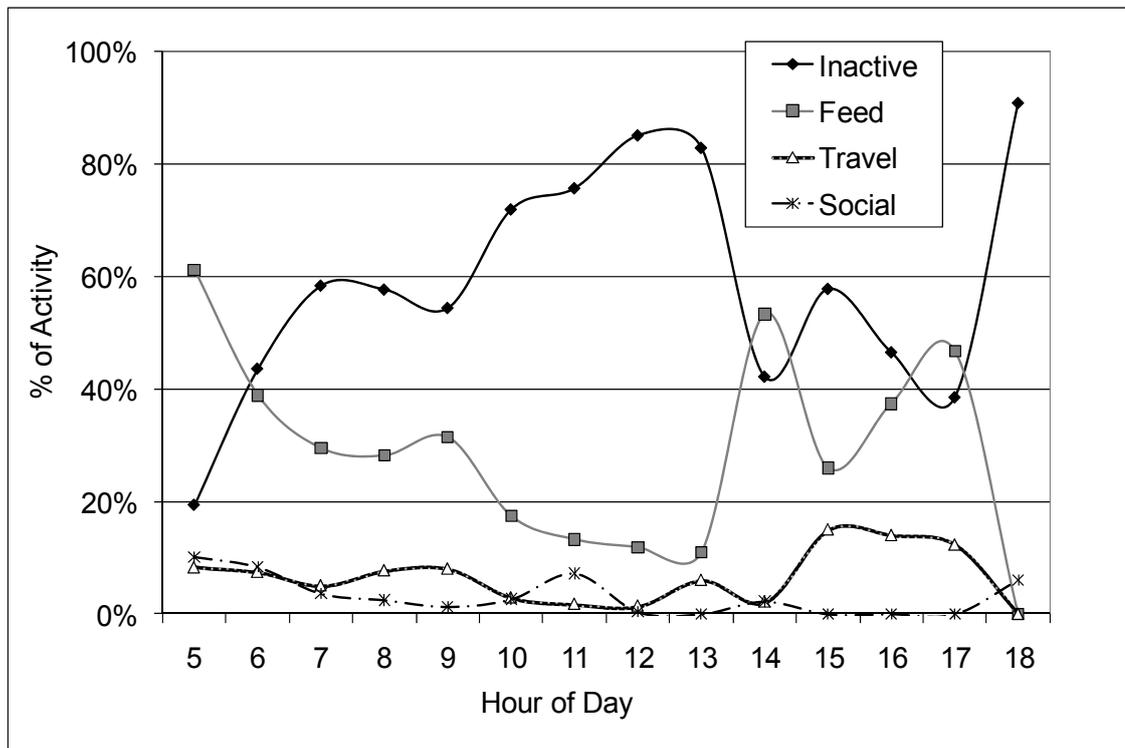
Activity	<i>n</i>	%	Sub-category	%
Inactive	2717	61.2%	Resting	94.2%
			Scanning	5.8%
Feeding	1204	27.1%	See Chapter 7	39.7%
Travel	282	6.3%	Quadrupedal	60.5%
			Jump	17.4%
			Brachiate	9.7%
			Climb	8.1%
			Drop	4.3%
Social	142	3.2%	Grooming	78.9%
			Vocalise	8.5%
			Play	5.6%
			Copulate	4.2%
			Dispute	2.8%
Other	98	2.2%	Autogroom	95.0%
			Defecate	3.0%
			Urinate	2.0%

**Table 5-1** Activity budget summary for *P. nigripes*. Activity category sample sizes include observations where no sub-category was attributable and therefore these may not match sample size in graphs containing sub-categories.

### *Activity pattern by hour in the day*

Looking at the *P. nigripes* activity cycle (Figure 5-4) we can see that activities were not evenly distributed throughout the day. Chi-squared tests for inactive, feeding, travelling and social behaviours show that inter-hour variations in these activities are non-random and highly significant in all instances; ( $\chi^2_{\text{inactive}} = 160.80$ ,  $\chi^2_{\text{feed}} = 227.02$ ,  $\chi^2_{\text{travel}} = 118.30$ ,  $\chi^2_{\text{social}} = 103.97$ ,  $df = 13$ ,  $p < 0.01$ ).

Doucs first became active at, or just before, sunrise (as determined by a GPS), which at the site was commonly around 5:30 am. After waking up, and an initial period of high activity, inactivity steadily became more prevalent as feeding behaviour decreased during the later morning. By 10 am resting dominated the activity budget with levels of 70-85% until 2:00 pm when activity increased and inactivity fell to levels between 40-60%. Finally, after 6:00 pm, activity had virtually ceased as animals prepared for sleep.



**Figure 5-4** Activities by hour in the day

Feeding frequencies were inversely related to inactive behaviour, with, grossly speaking, bimodal peaks in activity in the morning and afternoon. While the afternoon shows two peaks, one at 2:00 pm and one at 5:00 pm, the 2:00 pm peak may be caused by the small sample size from this period ( $n = 45$ ). Feeding began between 5:30 am and 6:00 am, with the earliest recorded feeding bout at 5:35 am, and continued at relatively high levels until about 10:00 am, at which time it dropped off to less than 20% of the activity budget. This lull lasted until about 2:00 pm when a second peak occurred, lasting until 6:00 pm, at which time feeding dropped off to zero.

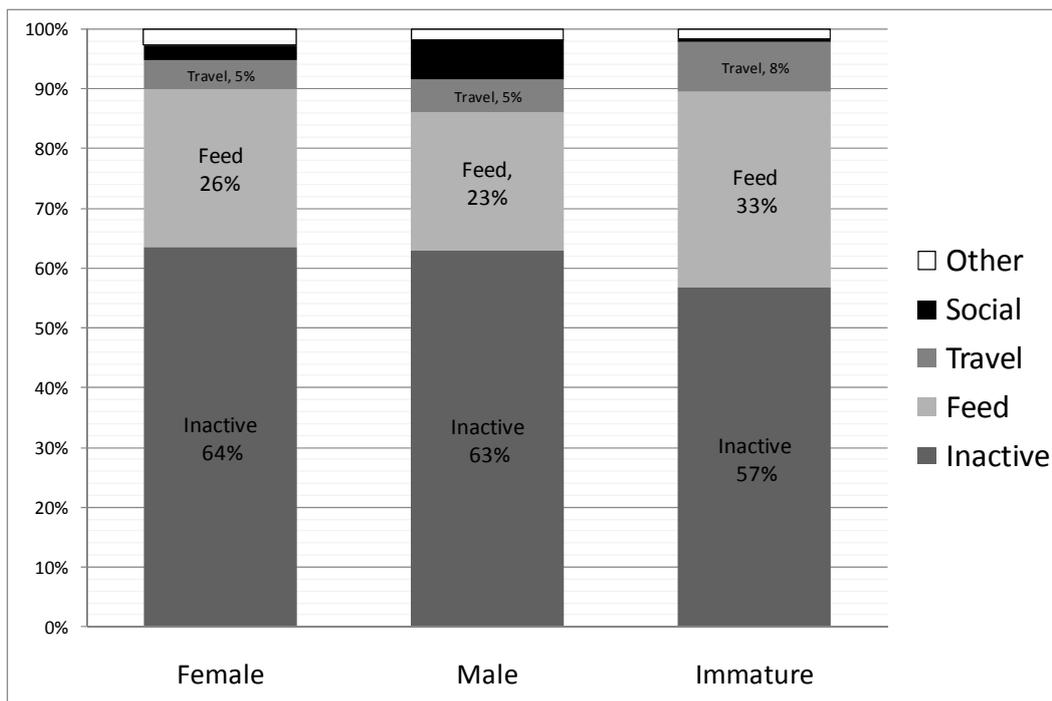
Travel frequencies were fairly constant at 7-10% over the morning period from the time of waking until the middle-of-the-day rest. During the rest period travel levels were very low until 3:00 pm when they spiked again as the doucs moved off from their resting places. Travel frequency remained relatively high throughout the afternoon at levels of 12-15%, only dropping off once the doucs reached their sleeping trees.

The frequencies of social behaviours were low throughout the day but showed three peaks. Firstly levels are high in the early morning between 5:00 am and 7:00 am, where they average around 8.5% of the activity budget. They then dropped off until another peak at around midday, where levels reached about 7%, corresponding with low levels

of movement and other activities at this time. Levels were low throughout the afternoon, when the doucs rest in their sleeping trees, until evening when frequency of social behaviours rose again. Social behaviour is dominated by grooming bouts, comprising over 70% of all social activities, and when considered separately (data not shown) show the same patterns as that of social behaviours in general.

### ***Age and sexual variation***

Activity budgets for adult males, adult females and immatures (juveniles and subadults combined) are shown in Figure 5-5. Infants are not included due to the very small sample size, but the small amount of information collected on infants was composed almost entirely of play behaviour. Activity budgets of males and females were not overly different; females spent slightly more time feeding and seemingly less time in social behaviours. Immatures differed from adult animals in activity budget in that they spent less time inactive and involved in social behaviours but more time feeding and travelling.



**Figure 5-5** Activity budget summary for *P. nigripes* by age and sex classes ( $n_{\text{female}} = 1380$ ,  $n_{\text{male}} = 1421$ ,  $n_{\text{immature}} = 645$ ).

## **Inactive**

There were no significant differences between age/sex classes in inactive behaviours ( $\chi^2 = 4.157$ ,  $df = 2$ , ns). Immatures spent slightly less time inactive than adults; both males and females showed similar frequencies of just over 60%. Variation in vigilance behaviour between sexes was very minimal, with adult males spending 6.7% and adult females 6.5% of the inactive period scanning. Immatures showed lower levels of vigilance, with 3.3%. If vigilance behaviour is considered in relation to the activity budget as a whole, rather than a sub-category of ‘inactive’, it comprises 4% for males, 4.1% for females and 2.1% for immatures. There was no significant difference between frequency of scanning behaviour in different canopy layers compared to generated expected frequencies for time spent in that layer ( $\chi^2 = 3.876$ ,  $df = 2$ , ns).

## **Feed**

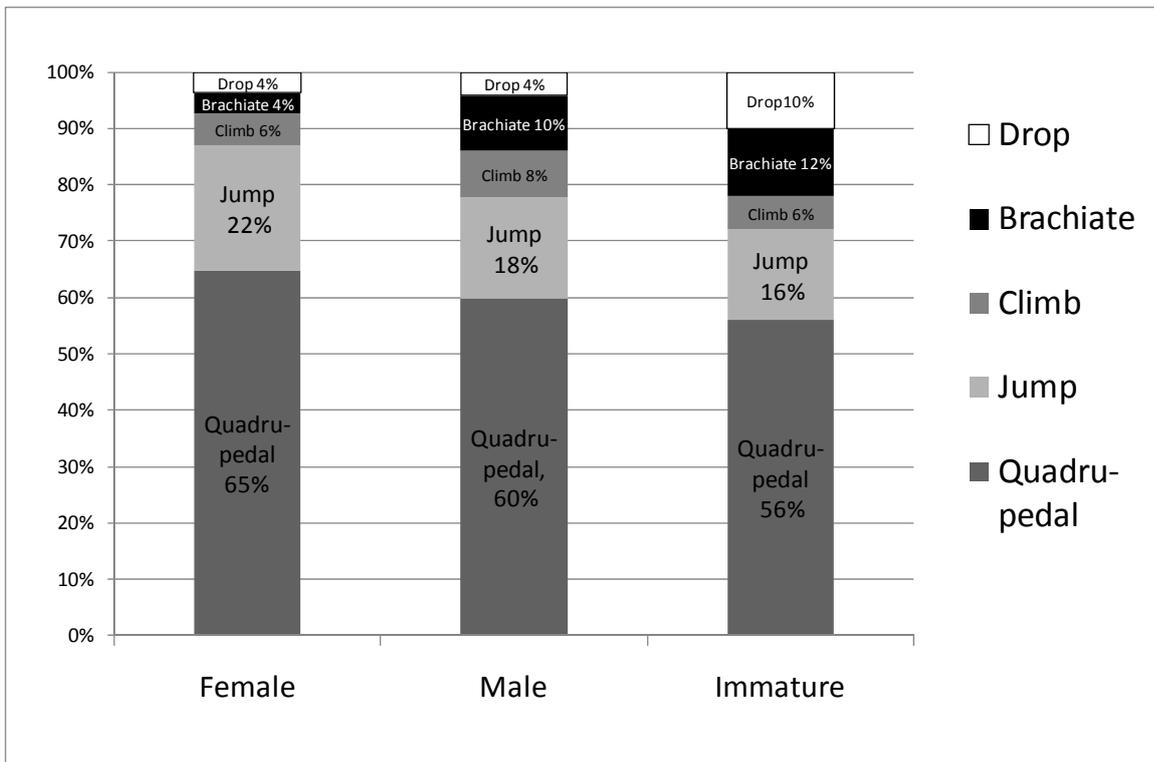
Some variation in feeding frequency was detected, with males feeding less than expected and immatures more ( $\chi^2 = 14.916$ ,  $df = 2$ ,  $p = < 0.01$ ). See Chapter 7 for a comprehensive analysis.

## **Travel**

Overall levels of travelling were significantly higher for immatures than for adults of either sex ( $\chi^2 = 9.803$ ,  $df = 2$ ,  $p = < 0.01$ ). For all age and sex classes, “quadrupedal” locomotion was the dominant form, comprising 55%–65% of all locomotory activity. This was followed by “jump” with frequencies of 16% to 22%. In both these categories, females had slightly higher levels than males, which in turn had slightly higher levels than immatures (see Figure 5-6). “Climb”, “brachiate” and “drop” locomotion types occurred at relatively low frequencies, and showed some variation between age and sex classes, although these figures may be due to small sample sizes. Frequency of climb was similar between all age and sex classes. Immatures brachiated with the highest frequencies (12%), followed by males (10%) and females (3.7%). Immatures also used drop as a form of locomotion more often than adult males or females (see Figure 5-6).

## **Social**

Males were apparently involved in significantly more social behaviour than females or immatures ( $\chi^2 = 57.736$ ,  $df = 2$ ,  $p = < 0.01$ ). Sample sizes for social behaviours are too small to make any reasonable comparisons between sexes for all categories except for groom, which is the major social activity for all age and sex classes. The larger number of instances of males being involved in grooming behaviour, 78 samples to females 32,



**Figure 5-6** Frequencies for travel by different locomotion types by age and sex categories ( $n_{\text{female}} = 54$ ,  $n_{\text{male}} = 72$ ,  $n_{\text{immature}} = 50$ ).

is responsible for females' relatively lower frequencies of social behaviour overall. In reality, the suggestion that males are more involved in grooming, and by extension social behaviour, is misplaced and results from the fact that focal animal sampling does not record dyadic interactions. Because grooming involves two or more individuals we can cross check this result and increase our data set size by including non-focal individuals. Results of such analysis show that males are not more involved in grooming behaviour than females, in fact the opposite appears to be true with 47.5% of grooming dyad samples including a female while only 38.8% involved a male. It therefore seems that unequal sampling of sex classes is responsible for higher levels of grooming and, by extension social behaviour, in males than females.

Looking at this expanded data set as shown in Table 5-2 we can see the relative amount of each age and sex class's passive versus active involvement in grooming dyads. Chi-squared test shows that frequencies of grooming between age/sex classes are not randomly distributed for either receiving ( $\chi^2 = 49.67$ ,  $df = 3$ ,  $p < 0.01$ ) or imparting ( $\chi^2 = 113.83$ ,  $df = 3$ ,  $p < 0.01$ ) grooming. Infants, while performing no grooming, received a total of 21% of all passive grooming bouts, all of them from adult females. Juveniles and subadults (immatures in Table 5-2) were seldom involved in grooming in

either an active or passive role, although they did spend more time grooming others than being groomed themselves. Males showed a large difference between active and passive grooming frequencies, receiving almost twice as much grooming as was given. Almost all grooming behaviour of males was given to and received from adult females. In fact, restricting analysis to only males and females, males received significantly more grooming than expected, or conversely males groomed females significantly less than expected ( $\chi^2 = 6.21$ ,  $df = 1$ ,  $p = 0.012$ ). Still, females received the vast majority of their passive grooming from males, although they split their active grooming behaviour between males and infants, males receiving over twice that of infants. Females imparted relatively far more grooming than they received by a factor of over 2.5.

	Infants (%)	Immatures (%)	Males (%)	Females (%)	Imparted Total %
Infants	0	0	0	0	0.0
Immatures	0	0	4.1	1.0	5.1
Males	0	1.0	0	25.5	26.5
Females	21.4	0	47.0	0	68.4
Received Total %	21.4	1.0	51.1	26.5	100.0

**Table 5-2** Percentage of grooming samples infants, immatures (juveniles and subadults), adult females and adult males received from and imparted to different sex and age classes ( $n = 98$ ).

### Other

Frequencies of “other” activities were similar between age and sex classes. With defecation and urination being relatively rarely observed, autogroom dominated in all classes. In relation to the activity budget as a whole, autogrooming comprised 2.5% of samples for females, 1.7% for males and 1.7% for immatures.

The inclusion of “nursing” in the other category is somewhat problematic, as this behaviour is obviously only exhibited by adult females and therefore makes comparisons across age and sex groups meaningless. To avoid this, nursing is considered separately from all other categories. This behaviour made up 1.5% of the adult female total activity budget, probably an under representation as nursing was noted as an activity only if the female was otherwise inactive. In other words, all other

activities took precedence over nursing except for inactive. Additionally, it was difficult to determine whether an infant was actually suckling or not.

Activity	Sub-category	Female	<i>n</i>	Male	<i>n</i>	Immature	<i>n</i>
<b>Inactive</b>		63.6%	878	62.8%	893	56.7%	366
	Resting	93.5%	579	93.3%	500	96.7%	351
	Scanning	6.5%	40	6.7%	36	3.3%	12
<b>Feeding</b>	See Chapter 7	26.4%	364	23.3%	331	32.7%	211
<b>Travel</b>		4.9%	67	5.3%	76	8.4%	54
	Quadrupedal	64.8%	35	59.7%	43	56.0%	28
	Jump	22.2%	12	18.1%	13	16.0%	8
	Brachiate	3.7%	2	9.7%	7	12.0%	6
	Climb	5.6%	3	8.3%	6	6.0%	3
	Drop	3.7%	2	4.2%	3	10.0%	5
<b>Social</b>		2.4%	33	6.8%	96	0.5%	3
	Grooming	97.0%	32	81.3%	78	33.3%	1
	Vocalise	0.0%	0	8.3%	8	0.0%	0
	Play	3.0%	1	1.0%	1	66.7%	2
	Copulate	0.0%	0	6.3%	6	0.0%	0
	Dispute	0.0%	0	3.1%	3	0.0%	0
<b>Other</b>		2.7%	38	1.8%	25	1.7%	11
	Autogroom	92.1%	35	96.0%	24	100.0%	11
	Defecate	5.3%	2	4.0%	1	0.0%	0
	Urinate	2.6%	1	0.0%	0	0.0%	0

**Table 5-3** Activity budget summary for *P. nigripes* by age and sex classes.

### ***Seasonal variation***

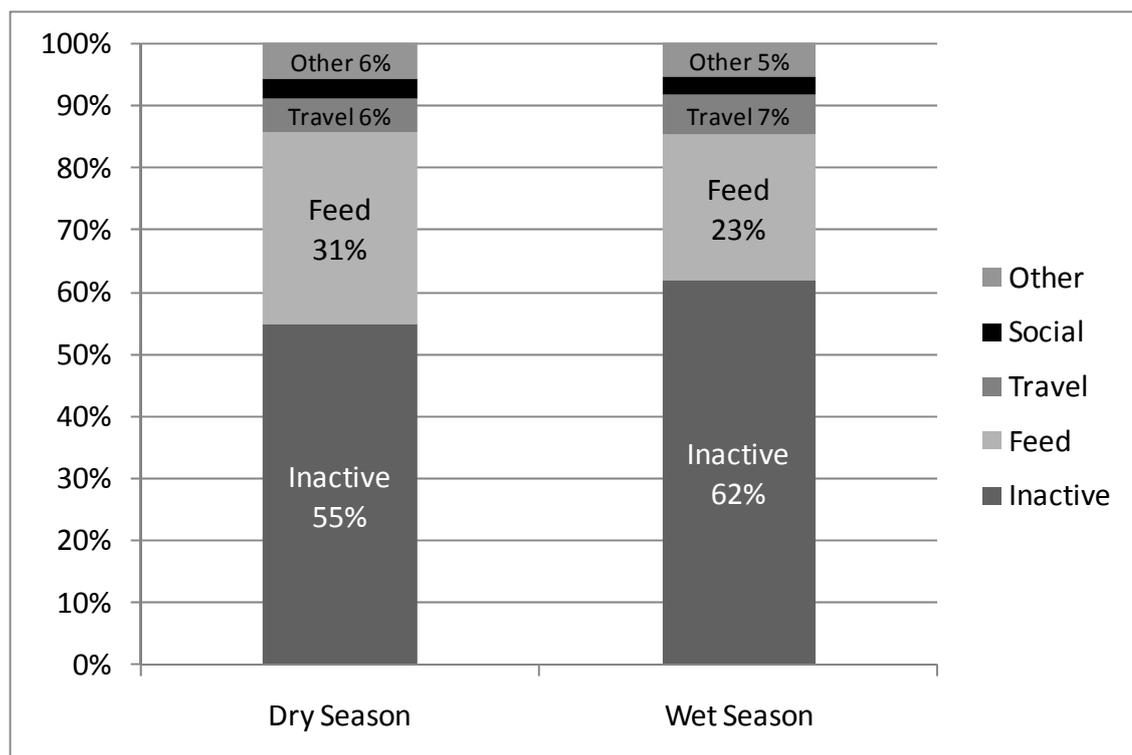
Because of the small size of the data set in some months, variation in activity budget throughout the year was done on a seasonal basis. The wet season was May through October ( $n = 2868$ ), while the dry season was November through April ( $n = 1722$ ). While more rain fell in April than October in 2003 (see Chapter 2) this is not generally the case as shown by rainfall figures collected by NOMAD from the region from 2000 to 2004.

Some variation in activity budget between wet and dry seasons can be detected in gross behavioural categories (see Table 5-4 and Figure 5-7). Animals spent more time inactive during the wet season than the dry, with respective levels of 61.9% and 54.8%,

although this did not reach significant values ( $U = 5.0$ ,  $p = 0.068$ ,  $n_{\text{wet}} = 5$ ,  $n_{\text{dry}} = 6$ , Mann-Whitney  $U$ -test). Conversely, less time was spent feeding in the wet season than

	<i>n</i>	Inactive (%)	Feed (%)	Travel (%)	Social (%)	Other (%)
Dry Season	1722	54.8	31.0	5.5	3.1	5.6
Wet Season	2868	61.9	23.4	6.5	3.0	5.2

**Table 5-4** Activity budget summary for *P. nigripes* by season.



**Figure 5-7** *P. nigripes* activity budget by season ( $n_{\text{dry}} = 1722$ ,  $n_{\text{wet}} = 2868$ ).

the dry, with levels of 23.4% and 31.0%, although again this was not significant ( $U = 10.0$ ,  $p = 0.361$ ,  $n_{\text{wet}} = 5$ ,  $n_{\text{dry}} = 6$ , Mann-Whitney  $U$ -test). Frequencies for travelling, social behaviour and other behaviours were similar between seasons.

Information on seasonality of breeding and births was insufficient to make any statements with assuredness. Ideally, data on seasonality in births would take a female to infant ratio by month if direct observations were missing; but it was rarely possible to sex all individuals in a group, so data were analysed on infant to adult ratio (bachelor groups and lone males excluded). Results (see Figure 5-8) show that infant to adult ratios were highest in five months of the year and zero in September through November,

although data sets were smallest for these months. Only one copulation bout was witnessed (see Copulation below for detailed description) which occurred in mid-July.

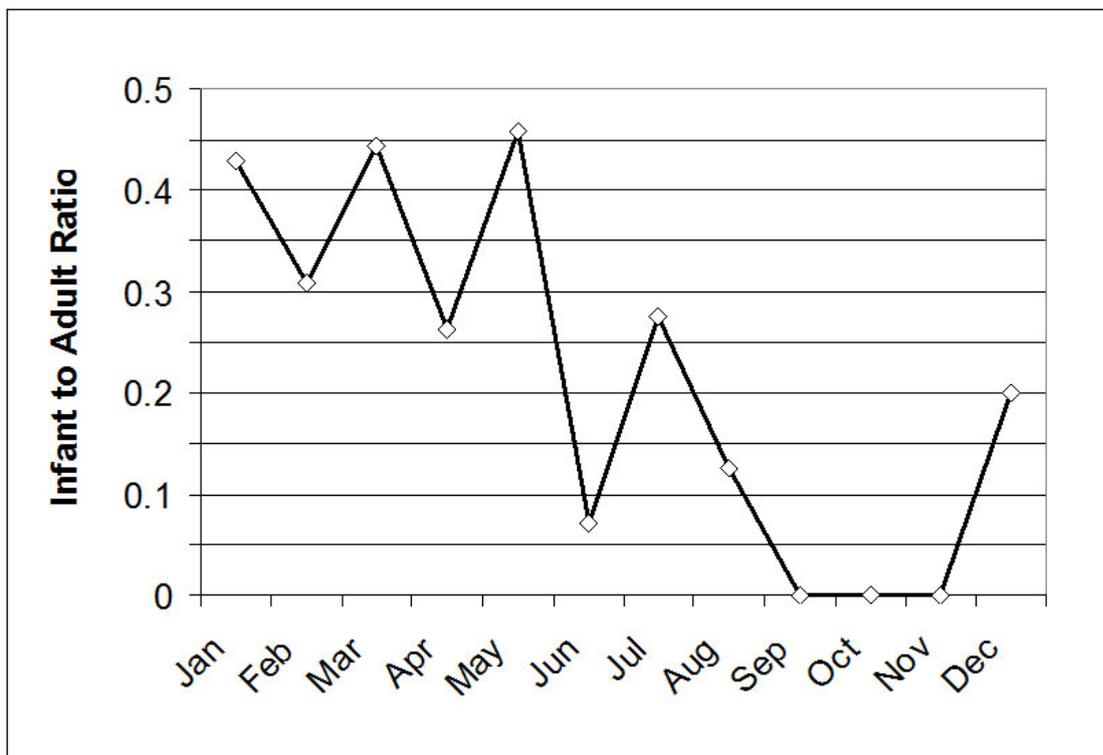


Figure 5-8 Monthly variation in infant to adult ratio in bisexual groups.

### ***Ad libitum behavioural observations***

In addition to behavioural observations taken using a focal animal, instantaneous sampling protocol, more complex and/or unusual behaviours were noted *ad libitum* in longhand format. Some of the more interesting behaviours are described in detail below.

### **Copulation**

Copulation was only observed once during the study period. This is described below using a combination of sample data and longhand field notes made by field assistant Mathew Preston:

*Date: 18/07/2004*

*Location UTM: 0709873/1356283*

*Weather: light rain to heavy downpour*

*Forest Type: mixed deciduous with bamboo understory*

*Group Size/Composition: 8 individuals: 1 adult male, 4 adult females, 2 juveniles, 1 infant.*

*Description:* Observation of the group started at 10:04 am. At 10:40:30 am the group became restless with frequent vocalisations, which continued on through the following period. The encounter occurred in the mid-canopy between two adults, one adult male and one adult female. Other members of the group moved to various surroundings during the mating session, with a very young individual venturing closest to the pair during mating. The surrounding individuals, particularly the juveniles, made a variety of vocal calls during this process.

The first mount occurred at 10:48 after the female approached the male and presented to him. It lasted c.20 seconds. This was followed by c.2 minutes where the male groomed the female. Animals then rested for some five minutes after which a second grooming bout began with both individuals grooming each other. This lasted 10 minutes and was followed by another short rest period followed by a second mount at 11:10 lasting 10 seconds. This in turn was followed by another grooming bout lasting 5 minutes, then another mount at 11:15 lasting 10 seconds and another very short grooming bout. Again rest followed for some 3 minutes followed by a fourth mount at 11:18:30 of 5 seconds and a very short grooming bout.

Almost immediately after the last copulation animals became antagonistic towards each other, seemingly initiated by the male. Animals pulled at each other, screamed, displayed teeth, chased, and acted aggressively in general. This lasted some 2 minutes and was followed by a short period of calm of just a few seconds, after which a fifth mount occurred at 11:21:30 am of about 5 seconds during which time the female struggled. The male then groomed the female which was later reciprocated but followed, after several minutes, by more antagonistic behaviour as described above. This culminated in the sixth mount at 11:25 am for about 8 seconds. Afterwards the male and female moved about 1.5 m apart and rested. 5 minutes later the male moved towards the female but she moved away. No further sexual behaviour was noted; the group was lost at 11:49 am.

Intercourse was very simple, with the male mounting the female from behind. Both parties ended individual mating sessions; either the male backed off, or the female pulled away. In between sessions, the individuals did a variety of activities dominated by grooming but including resting and feeding on nearby items. The animals also moved around on various branches in between copulations, but never went very far from one another (maximum estimated distance apart: 12 m).

### **Allomothering**

Parental behaviour other than that displayed by mother to infant was observed several times during the study period. A clear example of allomothering is described below using a combination of sample data and longhand field notes made by field assistant Adam Seward:

Date: 15/10/2003

Location UTM: 0709261/1356400

Weather: fine

Forest Type: mixed deciduous

Group Size/Composition: 10-20 individuals. 1? adult male, multiple adult females, >1 subadult, >1 juvenile, >1 infant.

Description: A large group of doucs had been followed since 10:44 am. After a period of a few minutes, during which the doucs were out of sight of the observer, they were spotted again moving through high trees c.30 m high in a less dense area of the forest. The doucs were travelling along a single path, of which approximately 100 m was clearly visible.

A female (Female 1) with infant on belly came into view and continued moving quadrupedally from right to left from the observer's point of view. The female then stopped and sat down on a large bough in clear view. The infant then climbed lower, appeared to attempt to suckle and then climbed onto the bough. The infant next walked quadrupedally about 2 m to another female (Female 2) sitting on the same bough (and to the rear with relation to the group's direction of travel). Female 2 picked up the infant and put it on her belly. An adult male then approached, sitting down between the two females, whereupon Female 1 moved away to the left (group's original direction of travel) and out of sight. After a few seconds, the male and Female 2 (with infant clinging on to her belly) also moved off in the same direction. The observer was too far from the group to hear any vocalisations that may have been made.

### **Paternalistic behaviour**

One example of male parental care (concerning a juvenile, not an infant) was also observed during the course of fieldwork, as documented by the author below:

Date: 04/07/2004

Location UTM: 0709873/1355986

Weather: fine

Forest Type: semi-evergreen

Group Size/Composition: 6 individuals. 1 adult male, 2 adult females, 1 juvenile, 2 infants.

Description: A group of 6 doucs had been observed since 6:41 am where they were detected sitting in a *Peltophorum cf. dasyrrhachis* tree (tag #223) feeding intently on seeds from its pods. A juvenile sat next to the focal adult male animal (who was clearly identified as such) while they fed for some 8 minutes. A female with infant then moved off to an adjacent *Peltophorum ferrugineum* tree (tag #93). A moment later the male moved to get up from his sitting position. He took the juvenile to his chest in one smooth action, unopposed by the juvenile, and leapt a gap of several metres to the adjacent tree after the female after which time they were out of sight (os).

## **Agonistic behaviours**

There were very few examples of agonistic behaviour observed during the course of the study. Despite this, there were single observed instances of several types of agonistic behaviour including presumed instances of resource defense, male defense of a breeding group from an all-male group, and peripheralisation of a subadult male. Examples of aggressive interactions are given below.

*Date: 31/03/2004*

*Location UTM: 0710024/1355920*

*Weather: fine*

*Forest Type: semi-evergreen*

*Group Size/Composition: several groups, see below.*

*Description:* Detect a group at 08:02 feeding on the figs of a strangling fig tree (tag #200) which is fruiting prodigiously, visibility poor, group size 4-8 individuals, composition unknown. 08:15 a second group detected sitting on the periphery of the fig tree, composition: 1 adult male, 2(?) adult females, 1 subadult male, 1 juvenile, 1 infant. 08:30 first group exits tree and heads east out of sight. 08:33 group 2 enters tree and begins feeding intensively. 09:08 a new individual appears from the north and tries to enter the fig tree. It is immediately chased out again and sits watching from a nearby tree. 09:11, another individual (unknown age or sex, not an adult male though) attempts to enter the tree along a large bough close to where subadult male and female (?) and juvenile feed. Subadult male goes and bars the way to the entering individual. Two individuals stand 2 metres apart and go rigid, even tails take on an angular aspect. Some low vocalising can be heard. 09:12 subadult advances and intruding individual backs off facing subadult male and then jumps/drops out of tree. Between 08:30 and 09:30 when the 2nd group left tag #200, there were several other altercations involving vocalisations and chasing behaviour, although none were seen in detail.

*Date: 04/07/2004*

*Location UTM: 0709885/1355995*

*Weather: fine*

*Forest Type: semi-evergreen*

*Group Size/Composition: Group A: 6 individuals. 1 adult male, 2 adult females, 1 juvenile, 2 infants.*

*Group B: 17+, all male group. 6+ adult males, 3+ subadults, 3+ juveniles.*

*Description:* Group A observed from 06:41. At 09:16 another group (group B) of doucs heard c.100 m SE. 09:37 group B closer and noisier, focal male of group A unresponsive. 10:37, groups about 40 m apart. Adult male group A begins frequently vocalising towards intruding group, occasional responses by male from group B. Continues for 10 minutes with occasional screaming from infant(s) from group A. 10:45 groups within 15-20 m. Adult male group A starts displaying. Crashes through nearby tree moving very quickly. 10:48 adult male group A very agitated, vocalises, scratches viciously with

hands at tree, head turning in all directions, group B still can not be seen though are very close. 10:49 infants screaming, a lot of locomoting. 10:53 group B goes silent. Male from group A moves, displaying, into tree between two groups then returns. 10:54 male repeats behaviour, group B still silent. 10:55 male abandons position and heads away after the rest of group A. 10:56 individuals from group B move in force into tag #96 and begin feeding.

Date: 02/05/2004

Location UTM: 0709932/1355761

Weather: fine

Forest Type: semi-evergreen - disturbed

Group Size/Composition: 6 individuals. 1 adult male, 3 adult females, 1 subadult male, 1 infant.

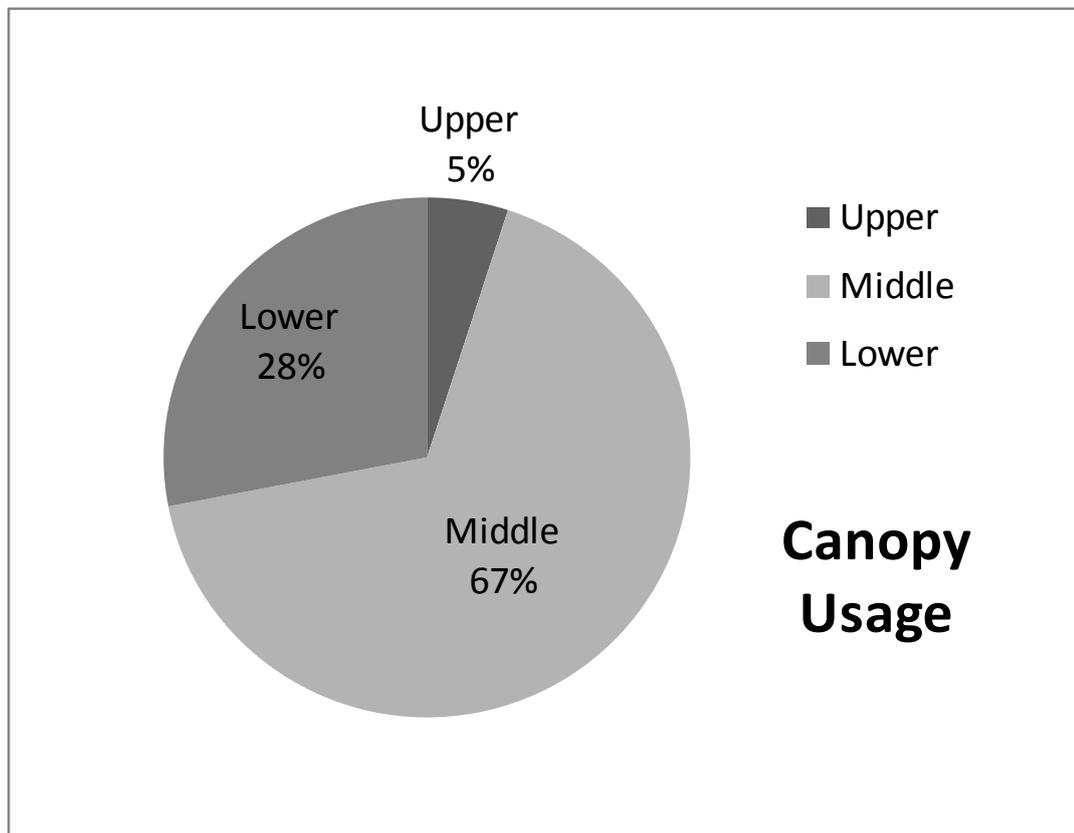
Description: Group detected at 17:05 feeding in tag #176 predominantly on seeds of fleshy fruit, tree is heavily laden. 17:15, adult male rushes at subadult male who is feeding some 7m away. Subadult moves away very quickly to very outskirts of the tree and both begin feeding again. 17:17, adult male rushes at subadult again and displaces him from the tree. Group, other than subadult, remain in tag #176 until 17:35 feeding. 17:37 group moves off to tag #187 and feeds for some 10 minutes then starts moving west, led by female with infant, with subadult coming last. 18:15 group enters large sleeping tree for the night. 18:19 subadult attempts to enter sleeping tree but immediately jumps quickly back into neighbouring tree (appears to have been chased out). 18:23 subadult moves back towards group's sleeping tree slowly. 18:28 too dark to see clearly.

## ***Canopy usage***

Location in the canopy during all activity samples was noted. Canopy layers were divided into "lower" (< 10m), "middle" (10 – 20 m) and "upper" (> 20 m), and the relative location of the focal animal was estimated. Chi-squared test shows that expected usage of canopy layers, all things being equal, is very different to actual usage ( $\chi^2 = 2613.163$ ,  $df = 2$ ,  $p < 0.01$ ); 67% of behaviours were performed in the middle canopy (Figure 5-9), while the upper canopy and lower canopy were severely under utilised, although the former less so, with respective frequencies of 28% and 5%.

Clearly, however, all canopy layers do not occur at the same frequencies. A rough scale of relative abundance of all canopy heights can be generated by using heights of trees from transects. There are several problems with this. Firstly, while tree height might give an indication of the stratigraphy of the forest, it gives no indication of the forest's density. The canopy of each tree will cover a range of heights depending on species, size, etc., which this can not account for. Secondly, only trees with a DBH of  $\geq 10$  cm

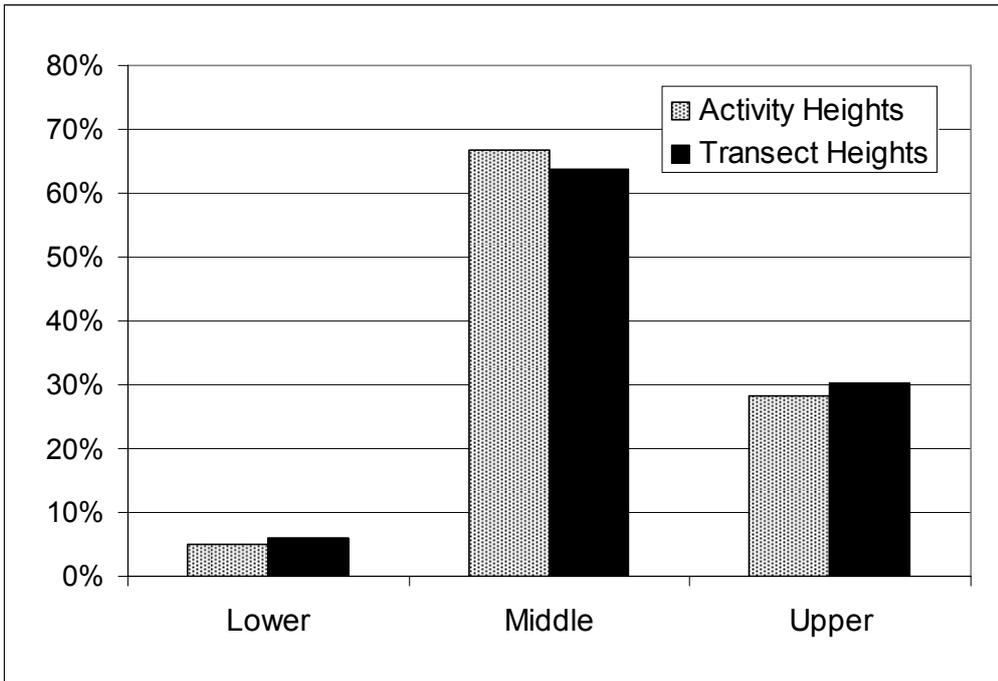
were included in transects but, there are actually many more trees and shrubs in the forest smaller than this arbitrary cutoff point. Both of these issues result in an underestimate of the volume of the middle and lower canopies with the presumed effect of overestimating the relative frequency that activities occur at these levels, especially the latter; it does however provide some basis for comparison.



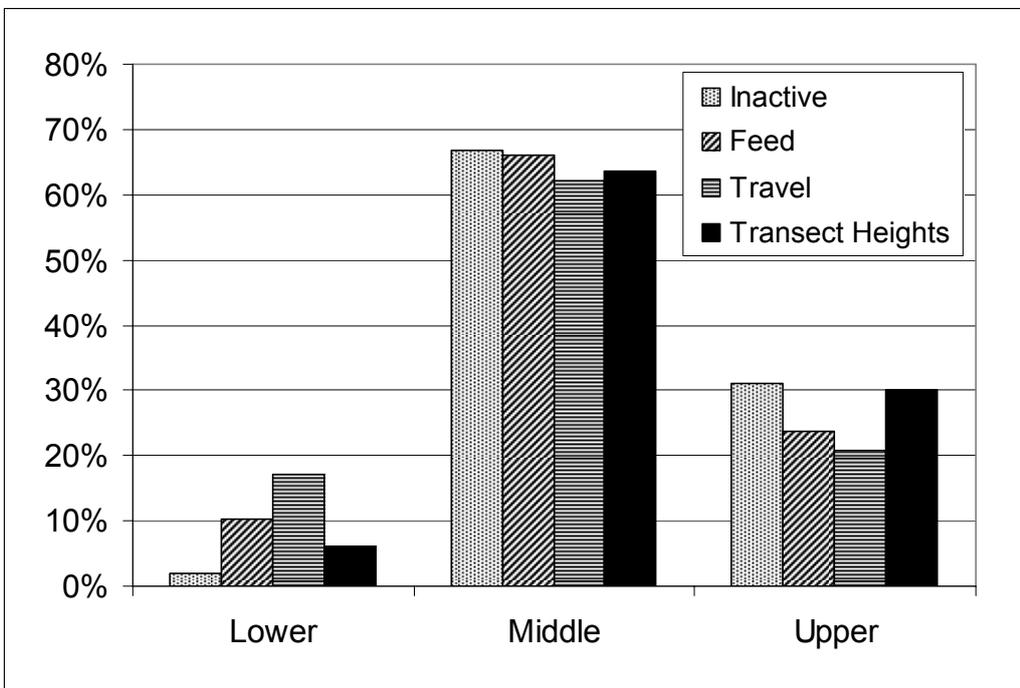
**Figure 5-9** Mean canopy usage for *P. nigripes* age and sex classes lumped ( $n = 4496$ ).

Even with this calibration, the effect is still significant, with doucs overusing the middle canopy relative to its abundance ( $\chi^2 = 19.283$ ,  $df = 2$ ,  $p < 0.01$ ). The effect, however, is very small as can be seen in Figure 5-10, with very little difference between transect tree canopy heights and usage of canopy layers.

Activities were analysed in their major categories (inactive, feed and travel) and canopy usage frequencies for these compared with expected frequencies derived from transect tree heights. There was a statistically highly significant association between activity types and canopy layer ( $\chi^2 = 194.036$ ,  $df = 4$ ,  $p < 0.01$ ). Strong positive associations were, travelling and feeding in the lower canopy, while strong negative associations were inactivity in the lower canopy, and feeding and travelling in the upper canopy. This can be seen in Figure 5-11.



**Figure 5-10** Canopy usage by *P. nigripes* ( $n = 4496$ ) compared with forest stratigraphy taken from transect tree heights ( $n = 394$ ).

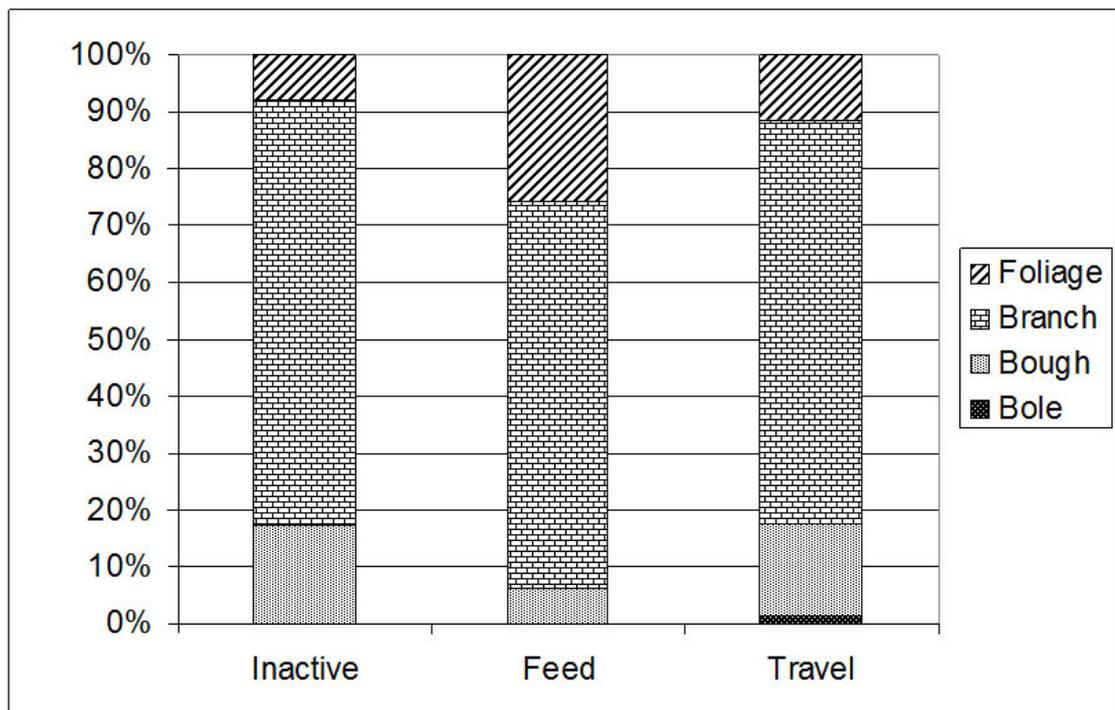


**Figure 5-11** Main activity budget categories stratified by canopy height and compared to transect tree heights ( $n_{\text{inactive}} = 2692$ ,  $n_{\text{feed}} = 1201$ ,  $n_{\text{travel}} = 269$ ,  $n_{\text{transect heights}} = 394$ )

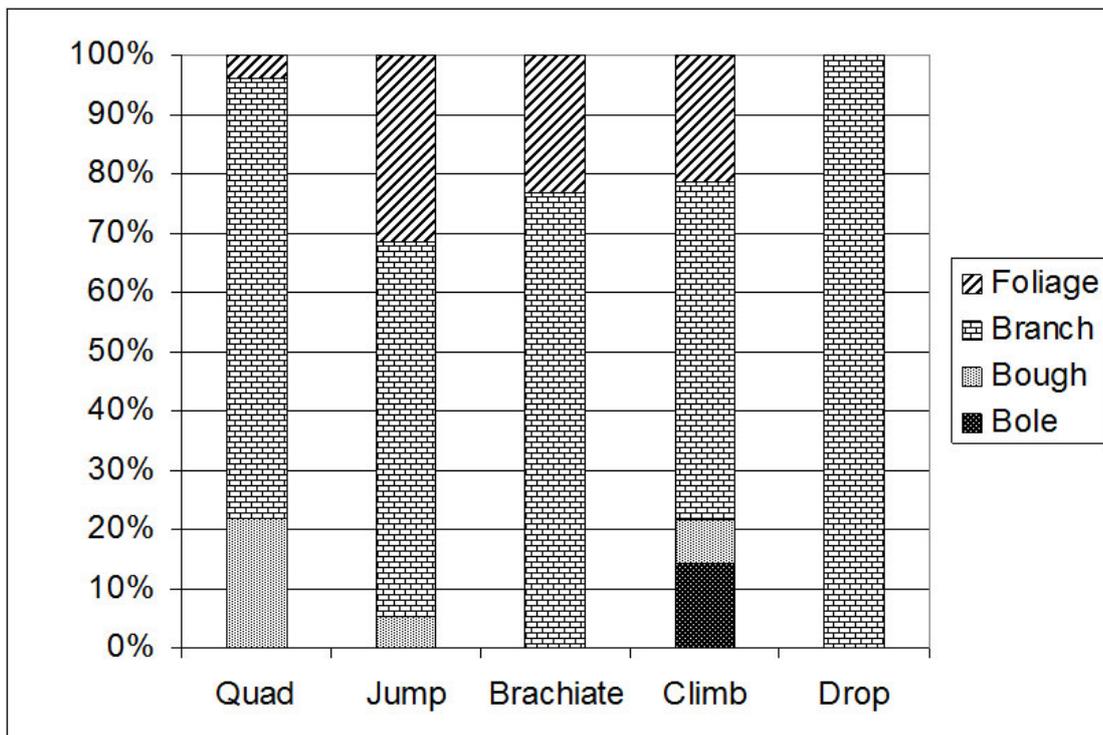
## Support usage

Branches are the most commonly used support (73.4%), with boughs (14.3%) and foliage (12.2%) fairly equally represented, and boles only very rarely utilised (0.1%). No independent measure of the relative availability of different supports was made although one can assume that in highest to lowest frequency they are: foliage, branches, boughs and boles (see Chapter 3 for definitions).

The relative usages of supports for each main activity category are shown in Figure 5-12. Inactive behaviours generally occurred on branches (74.7%) with lower frequencies on boughs (17.3%), foliage (7.9%) and boles (0.05%). Travel behaviour followed the same pattern, with branches utilised most frequently (71.1%) followed by boughs (16.1%) foliage (11.4%) and boles (1.4%). Feeding behaviour showed a slightly different pattern with branches still being the dominant support (68.0%) but, relative to other behaviour categories, a large percentage of activity occurring on foliage (25.9%) and a low percentage on boughs (6.1%).



**Figure 5-12** Main activity budget categories stratified by supports used ( $n_{\text{inactive}} = 1961$ ,  $n_{\text{feed}} = 742$ ,  $n_{\text{travel}} = 149$ ).



**Figure 5-13** Locomotion categories stratified by supports used ( $n_{quad} = 97$ ,  $n_{jump} = 19$ ,  $n_{brachiate} = 13$ ,  $n_{climb} = 14$ ,  $n_{drop} = 2$ ).

Differential use of supports for different locomotion types was analysed (Figure 5-). Quadrupedal locomotion occurred on all substrates except boles with branches dominating (74.2%), followed by boughs (21.7%) with a low frequency on foliage (4.1%). Jumps were usually made from branches (63.1%) but there was also a high frequency of jumps being made from foliage (31.6%) and relatively infrequently from boughs (5.3%). Brachiation events all occurred on smaller diameter supports, predominantly branches (76.9%) but also some in foliage (23.1%). Climbing behaviour occurred on all substrates most commonly in branches (57.2%), followed by foliage (21.4%), boles (14.3%) and boughs (7.1%). Dropping behaviour was rare and in all instances occurred from branches.

## Discussion

### *Inactive behaviour*

Doucs at the study site spent a large part of the day inactive, specifically the hours in the middle of the day. This is common among colobines (e.g. Oates, 1977, Marsh, 1981, Kunkun, 1986, Long Yongcheng *et al.*, 1998, Huang *et al.*, 2003) and may relate to the long periods of time it takes to digest leaf matter. Other studies which have looked at activity budgets in doucs have generally found lower levels than those presented here.

Three male *P. nemaus* in a semi-wild enclosure were found to have inactive levels of 49.3%, although they were released and studied for only 10 days, so it is possible that the novel stimuli from being out of the captive environment resulted in higher activity levels (Otto, 2005). Similarly, in a study in southern Vietnam, *P. nigripes* were found to rest at lower levels (42.93%) than the current study (Hoang Minh Duc, 2007). Immatures in the current study spent less time inactive than adults, which relates to continued activity through much of the midday rest period, as has been shown elsewhere (Hoang Minh Duc, 2007).

Like other activities, the middle canopy was where most resting took place. Inactive behaviour was very infrequent in the lower canopy, and more so if lower canopy availability was underestimated, as has been suggested. A preference for resting in the middle to upper canopy has been noted in other colobine species (e.g. Oates, 1977, Curtin, 1980).

Branches and boughs were the preferred supports for inactive behaviours, and this probably relates to the solidity of substrate required for these behaviours. Postures assumed when resting were similar to those previously depicted for *Presbytis melalophos* (Fleagle, 1980, p.204, fig.7-5), where individuals drape themselves sagittally over a bough. Additionally there was an upright sitting posture with legs splayed out in front of the body on supports, with the head resting against the chest. Animals would also occasionally huddle together, ventral-dorsal or ventral-ventral, and apparently sleep.

### **Vigilance behaviour and predation**

The amount of time spent in vigilance behaviour is largely related to predation risk, although the role of within-group vigilance in primates may also be significant (see Treves, 2000 for a review). Potential predators of doucs at the site may include raptors, pythons, and several species of cat. Although no instances of attempted predation were noted during the study, all of these animals have been shown to be potential threats to gibbons in Thailand (Reichard, 1998).

There are many records of raptors attempting to predate on primates, even larger bodied species ( Zinner and Pelaez, 1999, Liang-Wei Cui, 2003, Brockman, 2003, Colquhoun, 2006). Although it is rare, the black eagle (*Ictinaetus malayensis*) is a large raptor that occurs within the SBCA (T. Clements pers. comm.). This species may predate on

gibbons in neighbouring Thailand (Reichard, 1998), and its size (69-81 cm) (Robson, 2000) is similar to Verreaux's eagle (*Aquila verreauxi*) (76-81 cm) which appears to prey on hamadryas baboons (Zinner and Pelaez, 1999). Other smaller raptors within the area are the crested serpent eagle *Spilornis cheela* (56-74 cm) and the greater spotted eagle (*Aquila clanga*) (65-72 cm). Whether any of these raptors are capable of taking young doucs is, however, unknown, although one unconfirmed record of a douc being taken by an eagle of an unknown species does exist (Hoang Minh Duc, 2007). Doucs did not react to great hornbills (*Buceros bicornis*), which are considerably larger but do not predate on primates. Hornbills do, presumably mistakenly, elicit anti-predator behaviour in several species of monkey that are under predation pressure from raptors (Treves, 1999). The fact that doucs in the study did not react to hornbills suggests that pressure from raptors is low in the area.

Large snakes can also take primates (Burney, 2002, Ferrari *et al.*, 2004, Colquhoun, 2006). Within the region there are two species of python which could be potential predators, the reticulated python (*Python reticulatus*) and the Burmese python (*Python molurus*). No instances of interaction between snakes and doucs was witnessed, and it is likely that any effect that pythons may have on the population is very minimal (Bennett and Davies, 1994).

Doucs were occasionally seen to display increased and directed vigilance behaviour in response to alarm calls of other species, specifically two species of squirrel, the black giant squirrel (*Ratufa bicolor*) and the variable squirrel (*Callosciurus finlaysoni*) and, on one occasion, that of a red jungle fowl (*Gallus gallus*). In all instances these calls were a response to an unknown threat or the observer. Marmosets (*Callithrix geoffroyi*) (Searcy and Caine, 2003) and gibbons (*Hylobates lar*) (Reichard, 1998) have also been noted to react to the alarm calls of squirrels with anti-predator behaviours, and there are many instances of sympatric primates who respond to each others' alarm calls (Fleury and Gautier-Hion, 1997, Hardie and Buchanan-Smith, 1997, Oda, 1998, Fitchel, 2003). It is reasoned that for an animal to respond to other species' alarm calls suggests they are susceptible to at least some of the same predation pressures. Squirrels and red jungle fowl are presumably preyed on by a larger range of species than doucs, but there is presumably some overlap, judging by doucs' responses to their alarm calls. Exactly which species they share as predators is difficult to know: larger cats, pythons, raptors and humans are all potential candidates.

Overall, however, time spent in vigilance behaviour and the generally relaxed attitude to their surroundings suggests that predation risks are low for doucs. There was little difference in scanning behaviour between sexes in the study animals, although immatures had much lower levels than adults. Similar levels between male and female vigilance were found in *Nasalis larvatus* (Boonratana, 1993), but males were considerably more vigilant in both *Colobus guereza* (Fashing, 2001) and *Presbytis comata* (Ruhayat, 1983). Comprehensive comparison with other colobine species is difficult however, due to lack of data and apparently different definitions of the behaviour.

In some species, vigilance behaviour is more pronounced in the upper layers of the canopy, presumably due to the increased visible distance this affords. For example, males of *Trachypithecus obscurus* (Curtin, 1980) and patas monkeys (*Erythrocebus patas*) seek out tall trees for vigilance behaviours (Enstam and Isbell, 2004). This was not the case in the study animals, with vigilance behaviour being similar in all layers of the canopy.

### **Feeding behaviour**

The feeding ecology of the black-shanked douc is addressed comprehensively in Chapter 7. Some basic observations can be made here however.

There was a bimodal peak in feeding activity during the day, with the first peak in the morning and the second in the afternoon. As with the midday period of rest, this bimodal feeding pattern is common among colobines (e.g. Kunkun, 1986, Long Yongcheng *et al.*, 1998, Mukherjee, 2000-2001, Huang *et al.*, 2003), and, from what data are available, this seems to be the case in *Pygathrix* as well (Otto, 2005, Hoang Minh Duc, 2007). Red-shanked doucs in a semi-wild enclosure at the EPRC spent 33.7% of their activity budget feeding (Otto, 2005) while black-shanked doucs in Vietnam had frequencies of 35.04% (Hoang Minh Duc, 2007), both slightly higher than that found in the current study.

There was a strong negative association between feeding and the upper canopy. Lower than expected frequencies of feeding in the upper canopy are hard to explain, but may relate to greater volume (and therefore greater food abundance) than predicted in lower layers or possibly even avoidance of heat stress. Otto (2005) found that the vast majority of feeding bouts occurred below 10 m in a semi-wild enclosure at EPRC,

although no assessment of vegetation was performed, and so the relative availability of different canopy heights is unknown. This enclosure is on a limestone karst outcrop, with generally lower stature trees than that of the study site (pers. obs.).

Preferred supports for feeding were branches and, in approximately a quarter of all samples, foliage. Preferred food items such as new leaf and seed pods often occur terminally, and therefore this preference for smaller substrates while feeding compared to other activities likely represents the fact that animals are required to utilise these smaller supports to access these resources.

### ***Locomotion***

Doucs have been characterised as strictly arboreal (Lippold, 1998), and this was found to be the case during the study with one exception. A lone male was seen in a small tree some 4 m off the ground in an area that was a small plantation some 30 years previously. Trees in the area were of a very uniform size with canopies about 10 m high, and the canopy layer he was feeding in was largely isolated. He detected our presence soon after we detected him (we were only c.10 m distant) at which time he dropped to the ground noisily and ran off through the sparse understory.

Two other anecdotal reports of doucs coming to the ground in SBCA exist. One field worker reported seeing a small group of black-shanked doucs sitting on the ground next to a road (Kong Kim Sreng, pers. comm.), while another reported seeing several animals from a group of 7-9 individuals possibly foraging on the ground in semi-evergreen forest. They were observed for 3-5 minutes before the animals were disturbed (B. Hayes pers. comm.). In Vietnam black-shanked doucs have been seen to occasionally move terrestrially in areas of open forest (Hoang Minh Duc, 2007) and in one location they apparently spend a large amount of time on the ground (20%) on granite boulders (Nadler, 2008). These reports suggest that terrestrial locomotion is within the behavioural repertoire of black-shanked doucs, although clearly it is an uncommon event at the site where canopy closure is high.

Levels of travel were low during the midday period, which corresponds to high levels of inactive behaviours. In the afternoons, from 3:00 pm until sleeping, travel was at its highest. This relates to animals moving away from the areas in which they were feeding to find sleeping trees for the night, possibly targeting areas near rivers (see Chapter 6 for more details). Levels of travel overall were very similar to those found in a group of

semi-free-ranging *P. nemeus* at the EPRC in Vietnam (Otto, 2005) but lower than found amongst wild living black-shanked doucs in southern Vietnam (Hoang Minh Duc, 2007).

The low frequencies of travel in the upper canopy could be expected; as many of these trees will not have a canopy continuous with other trees (i.e. are emergents). Animals must therefore travel to lower canopy levels to make their way to other trees. It appears that this is the case as travel is over represented in the lower canopy, due to bias mentioned in the results section.

Branches and boughs were the two most preferred supports for travelling on, and this probably relates to the solidity of substrate required for locomotion. Supports were analysed for different modes of locomotion. Jumps were usually made from branches and also from foliage; this locomotion type was most commonly used to move between trees without adjoining canopies, hence the requirement to use smaller substrates at the more terminal parts of the tree. Quadrupedal and climbing behaviour was performed on all support types, and this is the dominant form of locomotion for doucs. Brachiation was usually on smaller supports, not surprisingly considering the restriction hand size plays in this mode of locomotion.

### **Brachiation**

Brachiation in doucs requires special attention. While it has long been recognised that doucs brachiate (Hollihn, 1973), it has been a renewed source of interest over recent years, as some researchers have stated that doucs can be classified as an intermediate or semi-brachiator, which can shed light on the transition from quadrupedal to suspensory locomotion in hominoids (Byron and Covert, 2004).

Data from captive red-shanked doucs (*P. nemeus*) has suggested that suspensory behaviour is very common in the species. One study found that over 10% of adult postures were suspensory in nature (Workman and Covert, 2005), while another returned values of 14.4% (Byron and Covert, 2004). No data were specifically taken on positional behaviour during the current study, although black-shanked doucs in Ta Kou Nature Reserve, Vietnam have been observed commonly feeding while using suspensory postures (H. Covert, pers. comm.).

Locomotion utilising suspensory behaviours was however recorded and reached frequencies of 9.7% for all age/sex classes combined, with immature individuals

showing the highest frequencies, followed by males and then females. Although sample sizes were small, frequencies were much lower than those found in the captive studies, which totalled 21.8% in one study (Workman and Covert, 2005), and 46% in another (Byron and Covert, 2004).

The reasons for these discrepancies may be twofold. Firstly, it is possible that the homogeneity of supports used in the enclosures for these captive studies (both performed at EPRC) positively biased the frequency with which animals would engage in suspensory behaviour. Most available substrates were 2-8 cm in diameter with no large diameter substrates available (Workman and Covert, 2005, U. Streicher pers. comm.), which contrasts to the large variation found in natural conditions. Substrates of this smaller size are ideal for brachiation, and probably less so for quadrupedal locomotion. Data from this study show that the vast majority of quadrupedal locomotion was performed on substrates larger than 5 cms in diameter, with very low frequencies on substrates less than this size (4.7%). Conversely, 23.1% of all brachiation events occurred on substrates less than 5 cm in diameter.

The relatively small size of substrates available in the captive study may not be overly functional for quadrupedal movement, while being ideal for brachiation. This would have the effect of negatively biasing frequencies of the first and positively biasing the second. While it is true that the other two species in the study, *Trachypithecus delacouri* and *T. hatinhensis*, managed to locomote quadrupedally in the vast majority of samples, this does not take into account the relative body weights of the species. Red-shanked doucs (*P. nemaesus*), especially males, are heavier (males 11.0 kg, females 8.2 kg quoted in Workman and Covert, 2005) than *T. hatinhensis* ( $\bar{x}_{\text{male}} = 8 \pm 0.39$  kg,  $n = 7$ ,  $\bar{x}_{\text{female}} = 7.4 \pm 0.44$  kg,  $n = 5$ ) or *T. delacouri* ( $\bar{x}_{\text{male}} = 8.3 \pm 0.1$  kg,  $n = 3$ ,  $\bar{x}_{\text{female}} = 9.2$  kg,  $n = 1$ ) (U. Streicher pers. comm.), and bulkier as well, meaning that quadrupedal movement may be more limited by supports of this size for doucs in these enclosures. However, it should also be noted that several aspects of skeletal anatomy in *Pygathrix* differ from those in *Trachypithecus*, and are more consistent with suspensory behaviour in the former (Covert *et al.*, 2004).

There may also, of course, be differences between *P. nigripes* and *P. nemaesus*, there being lower frequencies of suspensory behaviour in the former than those found in the latter in these captive studies (Byron and Covert, 2004, Workman and Covert, 2005). One possibility could be larger body weights in *P. nigripes* (K. Wright, U. Streicher

pers. comm.), although exact data on weights are lacking for the species. The fact that infants brachiated at higher frequencies than adults of either sex in the current study is somewhat suggestive that body weight may play a role in brachiation frequency.

These suppositions can not be tested with available data; it is clear however that more work is required to differentiate black-shanked doucs from other species, and wild from captive behaviours, in terms of suspensory postures and locomotion.

## ***Social behaviour***

### **Play**

Because infants were seldom used as focal animals, levels of play in activity budgets come exclusively from juveniles, subadults and adults. Amongst these age groups play was very uncommon, comprising only eight instances in 4,476 observations. Amongst three males of *P. nemaesus* in a semi-free-ranging environment, play behaviour comprised less than 1% (Otto, 2005) while over all age categories play comprised only 1.56% of the activity budget in wild black-shanked doucs in Vietnam (Hoang Minh Duc, 2007). This lack of play behaviour in doucs is perhaps not surprising as play in adults is considered to be rare among species that have high frequencies of social contacts between individuals (Pellis and Iwaniuk, 2000), as is the case among doucs. Play amongst adults in colobines is fairly infrequent in general, for example in white-headed langur (*Trachypithecus leucocephalus*) play comprised only 0.2% of activity budgets (Li and Rogers, 2005), while in *Nasalis larvatus* adults were never seen to play (Boonratana, 1993).

Play is rarely noted in adult captive doucs but is relatively common among infants and juveniles (Hollihn, 1973, Kavanagh, 1978, Ruempler, 1998). When adults are involved, they are generally a passive member of any interaction, in that they are jumped on or have their tails pulled. The reaction to this is generally ambivalence or moving away from the individual instigating the event (Hollihn, 1973). This was generally observed to be the case in the play behaviour of wild black-shanked doucs, with adults taking no active role except in two instances, one of which may have been a misinterpreted attempt at allomothering an infant. In this sense, play was usually a solitary activity.

Doucs were seen to engage in all three types of play: social play, locomotor play, and object play (Pellis and Iwaniuk, 2000). Social play involved infants and juveniles attempting to interact with adult individuals by jumping at them, crawling on them, play

biting them, etc. Locomotor play involved infants and juveniles, with the former clambering about for long periods of time with no apparent destination in mind, while the latter could often be seen to enjoy just leaping and jumping around in the canopy while adults rested or fed. This is reflected in the higher frequencies of locomotion in immatures' activity budgets. One adult and one subadult male were also seen actively interacting with their own feet, manipulating them with their hands and moving them around as in object play.

### **Grooming**

Grooming behaviour is generally treated as a good indication of social relationships and hierarchies among non-human primates. Grooming among the study subjects took up relatively small amounts of time relative to, for example, *Macaca* and *Papio* species where grooming may comprise 20% of the total activity budget (Dunbar, 1988). When this is compared to the 1.75% found during this study we can see that levels are quite low, although levels below 2% are standard for Asian colobines (Kirkpatrick, 2007) and similar to the 2.25% found for wild black-shanked doucs in Vietnam (Hoang Minh Duc, 2007).

Grooming behaviour was divided into three categories: autogrooming, passive involvement, and active involvement in a grooming bout. Autogrooming took up a relatively large amount of the activity budgets of all age and sex classes (see Table 5-3), although this seldom involved concerted cleaning behaviour; more often it was merely short periods scratching various parts of the body. Interestingly, no individual was ever seen to eat parasites or other matter removed during either autogrooming or allogrooming, which also seems to be rare in captive doucs (U. Streicher pers. comm.).

Most grooming bout dyads observed involved adult males and females (over 70%) as has been observed in captive doucs (Ruempler, 1998). Active grooming was not equally distributed between males and females, however, with females grooming males significantly more than vice versa. It is quite common for male colobines to receive more grooming than they impart (Newton and Dunbar, 1994). The only exception to this during the study period was during the observed copulation bout where the male groomed the female more than he received (see Sexual behaviour below). It has been shown, among female primates at least, that rank is correlated with amount of grooming received and that lower ranking individuals direct allogrooming at higher ranking

individuals (Schino, 2001). This is suggestive at least that the adult breeding male is dominant to females in the group.

Almost all other grooming dyads involved females and infants, with females always being the active participant. Captive (Ruempler, 1998) and wild (Hoang Minh Duc, 2007) studies suggest that this is a common grooming dyad among doucs and is best interpreted simply as infant care.

Interestingly, no instances of female-female grooming were observed during the study, although they have been amongst wild black-shanked doucs in Vietnam, although at what relative frequency is unknown (Hoang Minh Duc, 2007). Lippold (1977) in her 10 week study of wild red-shanked doucs found that female-female grooming was instead the most common allogrooming dyad, as has been noted in general among matrilineal colobine societies (Newton and Dunbar, 1994). Low levels of female-female grooming have, however, been noted in captive doucs (Ruempler, 1998). Female-female grooming dyads have been interpreted as a manipulation of female dominance hierarchies (Schino, 2001), with those species with strong hierarchies showing high frequencies of grooming between females and those with weak hierarchies showing low frequencies. As discussed more below (see Allomothering), no female dominance hierarchies were detected during the study. This lack of grooming and obvious dominance hierarchies among females suggests that dominance hierarchies are weak at best among female black-shanked doucs, and also raises the possibility that females within a group may not be related.

### **Aggression**

As discussed by Poirier (1974), any definition of the term aggression in animal studies is problematic as it involves an attribution of intent, obviously impossible in observational work on non-human primates. Our three examples of agonistic behaviour however can be fairly clearly attributed as such, and represent two instances of inter-group aggression including instances of resource defence and mate defence, and one instance of intra-group aggression, probably being an instance of the peripheralisation of a subadult male.

In general, aggression in colobines is low, especially within breeding groups (Poirier, 1974, Oates and Davies, 1994, Kirkpatrick, 2007). For example, Curtin (1980) recorded only two instances of aggression out of 252 social interactions in *Trachypithecus*

*obscurus*, Boonratana (1993) observed his study groups of *Nasalis larvatus* to spend only 0.7-0.8% of their activity budget engaged in such activities and Fashing (2001) recorded no instances of intra-group aggression in 16,710 scans among *Colobus guereza*. Information on doucs is largely absent in the literature, although amongst red-shanked doucs captive studies suggest low levels, with most instances lasting only a few seconds and with no records of injury (Kavanagh, 1978). In this study levels were similarly low, with only four observations from 4,443 samples.

### **Inter-group aggression**

One instance of inter-group aggression observed during the study, as detailed in Agonistic behaviours above, involved an interaction between a male of a one-male, multi-female unit and males of an all-male bachelor band. The behaviour of the breeding group male involved frequent vocalisations, displays and displacement behaviours which are common among primate species. Whether this represented an attempted takeover by the all-male group is unclear; but this is a common mode of male replacement among one-male, multi-female groups in colobines (Kirkpatrick, 2007) and it likely extends to *Pygathrix*.

A second instance of inter-group aggression occurred while a group was feeding in a fruiting *Ficus* sp. tree and individuals from another group attempted to enter the tree (as detailed in Agonistic behaviours above). While it is generally expected that aggression over food items will be rare amongst species that rely on readily available resources as in colobines (Whitehead and Jolly, 2000), fighting over favoured food items is one time when aggression between colobines can be quite intense.

Figs were obviously a favoured food among black-shanked doucs, with trees being heavily exploited when they came into fruit, as is apparently the case at other sites (Hoang Minh Duc, 2007). In this instance several groups visited this one tree during the morning, lining up for access, and once inside individuals gorged themselves on fruit. The heavy exploitation of such a resource is not surprising considering the fruit's high nutrient value (Janzen, 1979) and the importance of *Ficus* fruit as a source of calcium for forest animals (O'Brien *et al.*, 1998).

The relative rarity of *Ficus* sp. trees at the site, with none in the one hectare of forest represented by phenology trees, probably makes competition over this resource even more intense. This was demonstrated by the numerous altercations involving chasing

and displacing throughout observations of doucs in this fig tree, although most were obscured and it was difficult to tell whether they were inter- or intra-group. The definite observed instance of inter-group aggression over a food resource makes it clear however that doucs will defend and fight for key or favoured resources. This instance was particularly notable as it was a subadult male, not the adult male (and presumably the breeding male), of the bisexual group that defended the resource.

### **Intra-group aggression**

Intra-group aggression also occurs in wild black-shanked doucs, and in this study one instance observed involved the peripheralisation of a subadult male by an adult male (see Agonistic behaviours). In all colobine species studied to date maturing males leave or are forced from their natal groups, joining all male groups (Newton and Dunbar, 1994, Yeager and Kirkpatrick, 1998). Female dispersal may also be common among the Colobinae contrary to the pattern found among the Cercopithecinae (Yeager and Kirkpatrick, 1998). Lippold (1989) noted in captive red-shanked doucs that both sexes were peripheralised as early as one and a half years, but usually at two and a half to three years, which matches well with the observations of Ruempler (1998). Streicher (pers. comm.) also suggests that peripheralisation by the breeding male occurs when the juvenile is around three years of age generally, when the mother's next offspring is maturing. She describes it as follows:

As the second infant grows up, males might at some stage get very aggressive towards the juvenile. The juvenile keeps sitting on the cage floor and is hardly allowed to move, has no access to fresh leaves and is under a lot of social pressure (U. Streicher pers. comm.).

This description fits well with the observation from this study of a subadult male being threatened by the adult male in a breeding group. The subadult was displaced several times by aggressive means from a relatively large tree that was burgeoning with fruit. It was not permitted to travel with the group, having to trail behind, and was chased from the sleeping tree that the rest of the group entered for the night. This was the only observation of presumed peripheralisation witnessed during the study and so it is impossible to comment on whether females, as well as males, disperse in wild conditions from this evidence.

### **Vocalisations**

Most studied colobine species males make loud calls. For example *Trachypithecus obscurus* and *T. johnii* males gave territorial honks or booming calls in the mornings

(Poirier, 1974, Curtin, 1980) while *Presbytis melalophos* males give long calls throughout the day (Curtin, 1980). Black-shanked doucs' vocal repertoire runs contrary to these observations, as males lack a really loud call and in general all animals vocalise infrequently.

While lacking a loud call on the scale of many other colobines, male black-shanked doucs would make a guttural, throaty call on occasion. This call is perhaps best written phonetically as “goch” with a glottal stop, and was often done repeatedly, i.e. “goch-goch-goch”. This call could be heard from approximately 100-150 m, which is a considerably shorter distance than that achieved by most male loud calls (Wich and Nunn, 2002). The call was used in two apparent contexts: firstly, as a contact call between a male and the females in one-male units, and secondly, as an aggressive vocalisation either between males or directed at the observer.

In the first instance, this was occasionally heard in the mornings after a group woke up and seemed to be a contact call between the male and group females. The male would call and females would reply with a structurally similar but higher pitched vocalisation. This might go on for over half an hour and individuals were commonly moving during these vocal bouts, apparently attempting to come closer to each other.

In the second instance, vocalisations were commonly directed towards observers after they were detected. Although a female may give an initial warning call, it was commonly the male who would then take over and continue “barking”, or what Lippold (1977) called a “threat-warning bark”. This could go on for long periods of time, in one instance for 20 minutes, before the male moved off, although in this instance a female and juvenile were “stuck”, hiding in a tree close by the observer.

There were a few instances of males' vocalisations eliciting a response from other non-group males. It seems unlikely that in this context the loud call was used as a spacing mechanism, as these vocal interactions were more likely precipitated by other forms of detection first. Additionally, males in the vicinity did not always respond to the calling of other males.

I am unable to comment on the range of softer vocalisations made by doucs due to the necessary distance between the observer and the study animals. These were heard very infrequently and details were not noted. This low frequency of vocalisations has also been observed in captive red-shanked doucs (Ruempler, 1998).

## **Sexual behaviour**

As detailed in Copulation above, one instance of copulation was observed during the course of the study. As is the case in most colobines (Newton and Dunbar, 1994), the female solicited at least the first copulation by presenting to the male. A receptive female approaching the male for initiation of a copulatory bout has been noted among captive red-shanked doucs (Hollihn, 1973). Unfortunately, no detail was recorded on the female's body position during copulation (observed and described by a field assistant), but it has been noted among captive red-shanked doucs that the female is recumbent, pressing her ventrum against the substrate on which copulation occurs (Hollihn, 1973, Kavanagh, 1978). Intromission was observed to occur on six occasions over a period of 37 minutes. This runs contrary to Kavanagh (1978) who observed captive doucs to be single-mounters, although Hollihn (1973) classified them as multiple mounters. Lippold (1981) observed copulation multiple times in a single day and Ruempler (1998) noted that females copulated multiple times over an oestrous period as has also been observed at the EPRC (U. Streicher pers. comm.).

Each intromission lasted between five and 20 seconds and was broken off by either male or female. During copulation, harassment of the couple was not noted as it has been generally among other colobine species (Newton and Dunbar, 1994) and specifically among doucs (Hollihn, 1973, Kavanagh, 1978), although the group was clearly interested in the proceedings as evidenced by vocalisations and the close approach of an immature individual.

Aggression between the male and female was noted after the fourth intromission and continued between the following two intromissions with the female struggling throughout each. It has been noted in captive populations of the multiple mounting species *Colobus guereza*, *Nasalis larvatus*, and *P. nemaus* that the final mounts were often initiated by the male (Hollihn, 1973) as appeared to be the case here.

The female's reticence during the final bouts and the aggression between the pair seems to have been mitigated to some extent by grooming bouts as is commonly found among primates (Dunbar, 1988). In all instances the male initiated grooming after each intromission except the last, when no grooming took place. Over the course of the interaction grooming was quite equally distributed, with the male receiving grooming during 18 samples and the female during 19 samples. Compared to levels of grooming in non-copulatory situations, where the male grooms females at a quarter the frequency

as vice versa (data not shown), this represents an abnormally large investment by the male, suggesting a placatory function in this situation.

As douc females may copulate when they are not fertile, during both inter-oestrous periods and pregnancy (Hollihn, 1973, Brockman and Lippold, 1975), it is unknown whether this copulatory bout represented a conceptive or non-conceptive sexual interaction. While female ovulation is characterised by slight oedema and reddening of the sexual skin (U. Streicher pers. comm.), this is hard to detect, especially in field conditions. Furthermore, this reddening of the sexual skin and inner thighs is retained throughout pregnancy in red-shanked doucs (Ruempler, 1998), although the degree of reddening can be variable between individuals and intensifies in later pregnancy (U. Streicher pers. comm.). This redness of the inner thighs during pregnancy was confirmed for black-shanked doucs during the study, as it was evidenced by a different pregnant individual seen over several months.

Although most colobines breed throughout the year (Newton and Dunbar, 1994), including doucs (Lippold, 1989, Ruempler, 1998), various authors have suggested birth peaks for red-shanked doucs. In captive animals abroad, Lippold (1989) found a peak between January and August while Ruempler (1998) found peaks in February and April. Lippold (1977) estimated a birth peak in wild red-shanked doucs, based on knowledge of infants' ages from captive studies, to be between February and June, and some indication of this was found in wild black-shanked doucs in Vietnam (Hoang Minh Duc, 2007). Data taken from EPRC in Vietnam, where 12 doucs of various species have been born (Nadler, 2004), show that most births occur within the first six months of the year, although this area is considerably further north than the study site and no black-shanked doucs are included in the data set.

Data presented in Figure 5-8 of infant/adult ratios from this study suggest that a peak does occur in the first half of the year at the study site. Although highly speculative, assuming that the one copulatory bout witnessed was conceptive, it is possible to project forward to the possible time of birth. Red-shanked doucs' gestation period is probably about 210 days (Lippold, 1981), which would put the birth date in the first two weeks of February, again within the proposed birth peak.

## ***Parental behaviour***

### **Allomothering**

While infant transfer is rare in cercopithecines, with females being very possessive of infants (although see Chism, 2000), it is very common among colobines where transfer often occurs from the first days of life (McKenna, 1979, Newton and Dunbar, 1994). The possible reasons for infant transfer and the differences in this behaviour between the Colobinae and the Cercopithecinae have been discussed extensively. Earlier theories include that infant transfer helps train nulliparous females for motherhood, that infants may be adopted if their mothers die, that allomothering allows mothers to feed, that it increases group cohesion, or that it is simply a byproduct of maternal behaviour (see McKenna, 1979, Quiatt, 1979, and Newton and Dunbar, 1994 for comprehensive reviews), while more recently it has been suggested that allomothering permits faster maturation of infants and shorter inter-birth intervals for mothers (Mitani and Watts, 1997, Ross and McLarnon, 2000).

The phenomenon seems to be facilitated in most species of colobines by infants' bright or contrasting natal coat which attracts conspecifics (Fimbel, 1992, Newton and Dunbar, 1994, Ross and Regan, 2000). The natal pelage of black-shanked doucs is no exception, with infants being predominantly white in contrast to adults' mainly dark grey and black coats. In fact, the two colobines whose natal coat does not contrast with that of the adult, *Ptilocolobus spp.* and *Procolobus verus*, do not show allomothering behaviour (Newton and Dunbar, 1994).

Among captive doucs, infant transfer has been witnessed many times. Brockman and Lippold (1975) noted at San Diego Zoo that red-shanked douc infants were first transferred in the first week after birth, while Hill (1972) observed the phenomenon in this species mere hours after birth. Staff at the EPRC, Vietnam, where groups of *P. nemaus* and *P. cinerea* are housed, report that infant transfer is very common and occurs soon after birth (U. Streicher pers. comm.). This very early transference has also been noted among other species of colobine monkey (Hollihn, 1973, Nadler, 1997, Kumar *et al.*, 2005). Levels of transference among captive doucs increased in the weeks following birth, becoming especially common after three weeks (Brockman and Lippold, 1975), as has also been noted for other colobine species (Poirier, 1968, Kumar *et al.*, 2005). Transfers even included a juvenile male (Brockman and Lippold, 1975).

Infants often oppose transfer, reacting by screaming and squirming (Boonratana, 1993, Kumar *et al.*, 2005), especially if they are kept for extended periods of time or, not surprisingly, are abused (Jovanovic and Gouzoules, 2001). The nature of the transfer observed during this study, with the infant in effect controlling the situation by removing itself from one female without a struggle and moving to another female, is notable.

McKenna (1979) theorised that it was a lack of dominance hierarchies among female colobines that permitted allomothering to develop. No dominance structure was evident among female doucs in this study, although these can be hard to detect amongst colobines (Poirier, 1974). Evidence from captive studies is contradictory, with Ruempler (1998) stating that no dominance hierarchy existed among female captive red-shanked doucs, while Hollihn (1973) suggested that it did, based on food snatching behaviour. In wild conditions, however, disputes over preferred food items is very rare due to greater availability of resources, although *Ficus* sp. fruit is an exception (see Aggression).

The casualness of the witnessed transfer may be a further indicator of the lack of a dominance structure among female black-shanked doucs. Furthermore, this instance of infant transfer is suggestive that douc groups are matrilineal in nature. Newton and Dunbar's (1994) comprehensive assessment showed that the only colobines identified as not displaying infant transfer, *Ptilocolobus spp.* and *Procolobus verus*, were also the only species having a patrilineal social structure. In this environment of matrilineal social groupings, allomothers are increasing their inclusive fitness by providing care. This pattern of weak female dominance structures and matrilineal social groupings as a correlate for allomothering behaviour extends to Cercopithecines also (Chism, 2000).

Regardless of the theoretical implications of infant transfer, the one established and several ambiguous instances of this behaviour observed during the study confirm that allomothering occurs in wild living black-shanked doucs. Conversely, the phenomenon of babysitting behaviour, where a single individual will oversee several infants, was not witnessed during this study but has been reported for captive doucs (Hollihn, 1973) and other colobines (Curtin, 1980).

### **Paternalistic behaviour**

Male parental investment is difficult to assess in wild non-human primate populations as the paternity of any individual is seldom known and therefore the term “paternalistic”, meaning interactions between adult males and immature individuals, is used here (Bales, 1980). Such behaviour by males toward immature individuals may reflect an investment in offsprings’ viability through enhanced survival or through rank acquisition (e.g. Buchan *et al.*, 2003), or an attempt to procure more matings at a later date through demonstrated investment to females (van Schaik and Paul, 1996).

Paternalistic behaviour has been divided into five types: toleration, protection, play, grooming and nurturing (see Bales, 1980 for definitions). Amongst the study subjects, males tolerated infants and juveniles who jumped on them during play, although they took no active role (as described in Play) and so could not be said to engage in the third type of paternalistic behaviour. There was no evidence of protection behaviour as defined by Bales (1980), although at no time was an infant seen to be directly threatened by other individuals. Males were never seen to groom infants, although one instance of grooming a juvenile was witnessed; this seems to be a rare event.

The instance of an adult male carrying a juvenile between tree gaps, as described in Results, falls within one of the last two categories of grooming or nurturing, as Bales (1980) defines short-term carrying and cradling in the former while protracted bouts are categorised under the latter. This seems an odd distinction, as clearly carrying behaviour implies nurturing (provided all individuals are willing participants). Bales (1980) suggests that these paternalistic behaviours can be scaled so that if, for example, any species showing nurturing behaviour would generally show all other behaviours below this. This being the case, the lack of evidence for protection in the study may therefore be an artifact of observational bias rather than an actual absence, although it should also be emphasised that no evidence for infanticide was collected during the study.

In captivity, Streicher (pers. comm.) notes that strong and immediate protection of infants and juveniles by the male does occur, elicited by approach towards the individual by an “intruder” and a warning vocalisation by the female. If the female tolerates the intruder, usually a keeper, the male will generally not react. This protection response lessens as the infant gets older. This suggests at least that infanticide may be an issue among doucs.

Comparative evidence from captive animals suggests that these observations are generally valid. Adult males are tolerant of play behaviour, but are rarely actively involved (see Play), and have been seen to provide “comforting behaviour” for frightened juveniles, and one individual “sought-out, cradled and groomed” infants (Brockman and Lippold, 1975 pp 128). Streicher (pers. comm.) notes that paternalistic behaviour is quite variable among individuals, with some individuals involved in carrying infants at an early age while others do so only at very low frequencies. Further, males may become a preferred sleeping partner once a juvenile’s mother gives birth to a new infant. Therefore, while paternal behaviour may be minimal and somewhat discontinuous, it is certainly expressed in a number of ways in doucs and is more common than in some other colobine species, e.g. *Trachypithecus hatinensis* (U. Streicher, pers. comm.), at least in captivity.

## Summary

For black-shanked doucs at the study site the day usually begins at or just before sunrise. Depending on the distance between individuals in the group, the group might be brought together by contact calls between the male and females. When the group is somewhat cohesive again they move off to find a suitable feeding site. Feeding in the morning is very intensive and dominates all other behaviour. It continues for several hours with more or less movement between trees, seemingly dependent on the size of food patches, until hunger is apparently sated.

The later morning and early afternoon, after this initial gorging, are dominated by inactivity. Individuals sleep or rest in the canopy, sometimes in close proximity to others, in a variety of poses, occasionally feeding from the tree in which they are resting. Occasional social behaviour, such as grooming, occurs most frequently during this period, and play is often continued throughout this time by infants and juveniles. In the mid to late afternoon, the group becomes more active again, usually moving off from their resting site to feeding trees in a different area where they again feed intently for some time. Before sunset, the group will move off again to find a sleeping site, where they generally remain inactive as night closes in.

At this point there seems to be little seasonal variation in activities, but further study with larger data sets may modify this finding. Age/sex classes showed some variation, with males feeding less than females and immatures more, while immatures engaged in

more locomotion than either sex of adult. Socially, males and females dominated grooming activities, with males receiving more bouts from females than they imparted.

Evidence is also presented for rarer social behaviours including allomothering, male parental investment, peripheralisation of a subadult and copulation. Agonistic encounters are rare, especially intra-group, although extra-group aggression does occur in some instances such as between one-male groups and bachelor groups, or over prized resources such as fruiting fig trees. Therefore, while frequencies of social behaviour are low, a rich behavioural repertoire is available. Further studies focusing on behaviour would likely unearth many more social interactions than presented here.



## ***Group size, group composition and ranging behaviour***

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### **Introduction**

To date there is very little information about the group dynamics of black-shanked doucs (*Pygathrix nigripes*), with most information coming from general surveys composed only of group counts as opposed to long-term socio-ecological observations, with the notable exception of that of Hoang Minh Duc's (2007) recent work. These have generally suggested that group size can be highly variable in the species, from as small as one up to 50 individuals and all sizes in between (e.g. Long, 2000, Ha Thang Long, 2002, Ngo Van Tri, 2003a, Hoang Minh Duc, 2007).

This large variation in group size may be related to several factors. Firstly, it has been hypothesised that group size is positively correlated with habitat quality (Lippold, 1998), with disturbed habitat returning low group numbers. This relationship is detailed in the ecological-constraints model, which posits that as group size increases, so too does intra-group feeding competition. In this model, the larger the group, the further it has to range in order to find sufficient resources to sustain the group. Maximum group size is therefore constrained depending on the availability and distribution of resources within the environment (Wrangham *et al.*, 1993, Chapman *et al.*, 1995, Janson and Goldsmith, 1995, Gillespie and Chapman, 2001, Chapman and Pavelka, 2005). While the applicability of the model has been demonstrated for some frugivores, the generality of the model as it applies to folivores has not yet been consistently demonstrated (Yeager and Kirkpatrick, 1998, Gillespie and Chapman, 2001).

Secondly, based on patterns within Asian colobines in general, and specifically within the odd-nosed colobines, it has been hypothesised that doucs may have a fission-fusion social structure (Kirkpatrick, 1998, Hoang Minh Duc, 2007). Short-term observations of the red-shanked douc (*P. nemaeus*) originally suggested that the species forms both one-male units (OMUs) and multi-male units (MMUs) (Gochfeld, 1974, Lippold, 1977), but since these studies most reports have suggested that the species occur in MMUs (Lippold, 1995, Lippold, 1998). Recent studies on *P. nigripes* have suggested that OMUs are the predominant social grouping, although MMUs have also been noted (Hoang Minh Duc, 2007). Multi-tiered social structures can be difficult to determine

based on short periods of observation. Indeed, *Nasalis larvatus* was assumed to form MMUs until long term studies were conducted; the long term studies showed the basic grouping to be OMUs that come together to form bands (Kirkpatrick, 1998).

The primary aims of this chapter are, firstly, to characterise grouping patterns in black-shanked doucs at the study site and, secondly, to identify the correlates of group size – specifically to identify if the species shows a fission-fusion social structure, and whether habitat quality correlates with group size. Other topics which are briefly addressed include ranging behaviour and use of sleeping sites.

## Methods

Analysis of group size and its variation in relation to habitat quality were based on two data sets. The first data set comes from observations made around the Camp 6 study site. Only observations with good estimates of the number of individuals within a group were included; i.e. those where observed and estimated group size were similar or the same. Wherever possible, multiple counts of the same group were removed, although this only pertained to one group that was recognised on multiple occasions and, as such, some groups are probably included more than once in the data set.

The second data set comes from surveys conducted across Seima Biodiversity Conservation Area (SBCA) performed by the Wildlife Conservation Society (WCS), collected between 1/4/2000 and 9/5/2004. I was not part of these surveys. These surveys covered a much wider area than the Camp 6 study site, and therefore may offer a better idea of the diversity of group size for the species. Some sightings from this data set were opportunistic, but most were made while walking transects within the core monitoring area of SBCA (see Figure 6-1). WCS transects were walked during the dry season (December-March) several times per year searching for both wildlife sightings and track and sign. Potential issues with the SBCA-wide data set include the fact that data on group composition were not taken and, as many surveyors were involved in collecting the data ( $n = 11$ ), there may be considerable inter-surveyor error.

Data collected in both data sets included the date, observer, UTM location as determined by GPS, minimum group number and estimated group number. For analysis of group size, lone individuals and groups containing only males, as discussed in “Unmated males” below, were discarded, as were incomplete or sign data entries (those

records where direct observations were not made). A test for homogeneity of group sizes from the two data sets was conducted using the Mann-Whitney *U*-test.

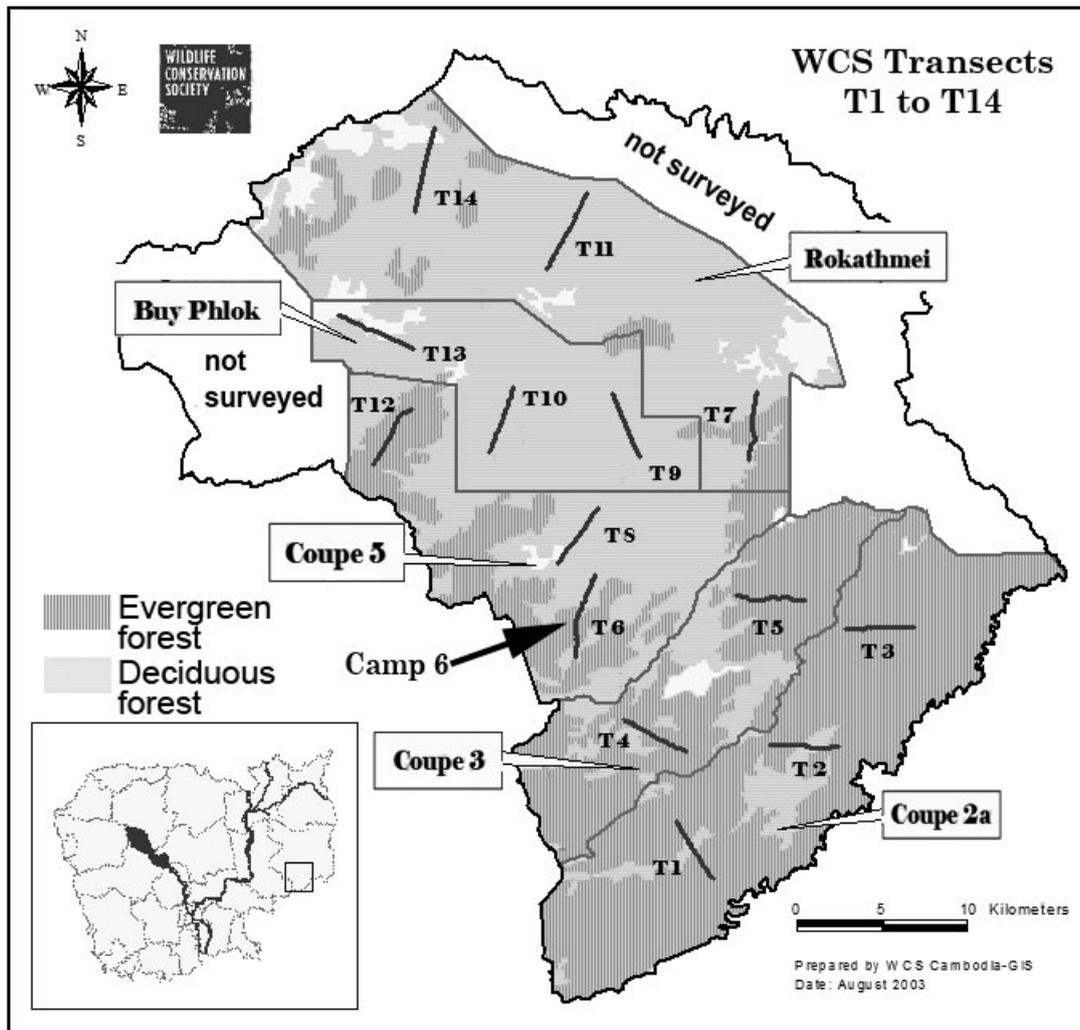
In order to ascertain the effect of habitat type on group size, each encounter from the SBCA data set was input into a GIS (ARCMAP 9.2); a 200 m and 500 m buffer was created around it and the buffer was then clipped. A buffer of 100 m was also created around permanent water courses as the Japan International Cooperation Agency (JICA) digital data set (2003) is of insufficient resolution to pick up riparian forest (Rawson *et al.*, in press). The amount of evergreen/riparian, semi-evergreen and deciduous forest in each clipped buffer was then calculated and the correlation between group size and each habitat type for all encounters calculated using Pearson's product-moment correlation coefficient in SPSS 11.5. An additional *t*-test was performed between group size in homogenous areas of the two most extreme habitat types, evergreen and deciduous forest.

Group density within different habitats was calculated using encounter rates on each of 14 transects monitored by WCS staff (see Figure 6-1) based on data from 2003 (walked twice), 2004 (walked twice) and 2005 (walked three times). Transects were straight to reduce the chance of multiple counts of the same group on a single walk. Encounter rates were calculated as the number of groups encountered, divided by the length in km for the transect, averaged across years. The area of each forest type around each transect was then determined using a GIS (ARCMAP 9.2). A buffer of 50 m was used around each transect, as this is the effective strip width determined through distance sampling analysis (Pollard *et al.*, 2007). Correlation between forest type and encounter rate was then calculated using the Pearson product-moment correlation coefficient in SPSS 11.5.

Wet season (May – October) versus dry season (November – April) variation in group size was assessed from Camp 6 data only as SBCA-wide data were collected only in the dry season. Comparisons were made using the Mann-Whitney *U*-test. Sightings of lone individuals, counts with low confidence and, where possible, multiple counts of the same group were removed from the data set.

To assess day range, a new location was taken every half hour that a group was in observational contact, or when they moved appreciably. Location was based on the focal individual when focal sampling was possible but on the centre of the group when no focal individual was available (Isbell *et al.*, 1999). The number of full day ranges

was minimal as animals were usually lost at some time during the day, most commonly because they detected the observer. Due to paucity of these data, mean hourly ranges were calculated based on any series of observations of a single group which had more than one consecutive location datum. These were not stratified by hour of the day due to lack of data, but were averaged over the entire active period.



**Figure 6-1** Map of SBCA showing WCS transect locations (courtesy of WCS – Cambodia). Camp 6 (arrowed) is located to the west of the centre of Transect 6 (T6).

Sleeping trees were located and measured on an opportunistic basis. To test whether the location of sleeping trees was random relative to rivers, the distance of each sleeping tree to the nearest river was determined using ARCGIS 9.1 and categorised as either within 75 m, 150 m, 300 m or 500 m. The same was done with all recorded feeding trees to provide a comparative measure. To test whether the size of trees were randomly selected, comparisons of height and diameter at breast height (DBH) of sleeping trees

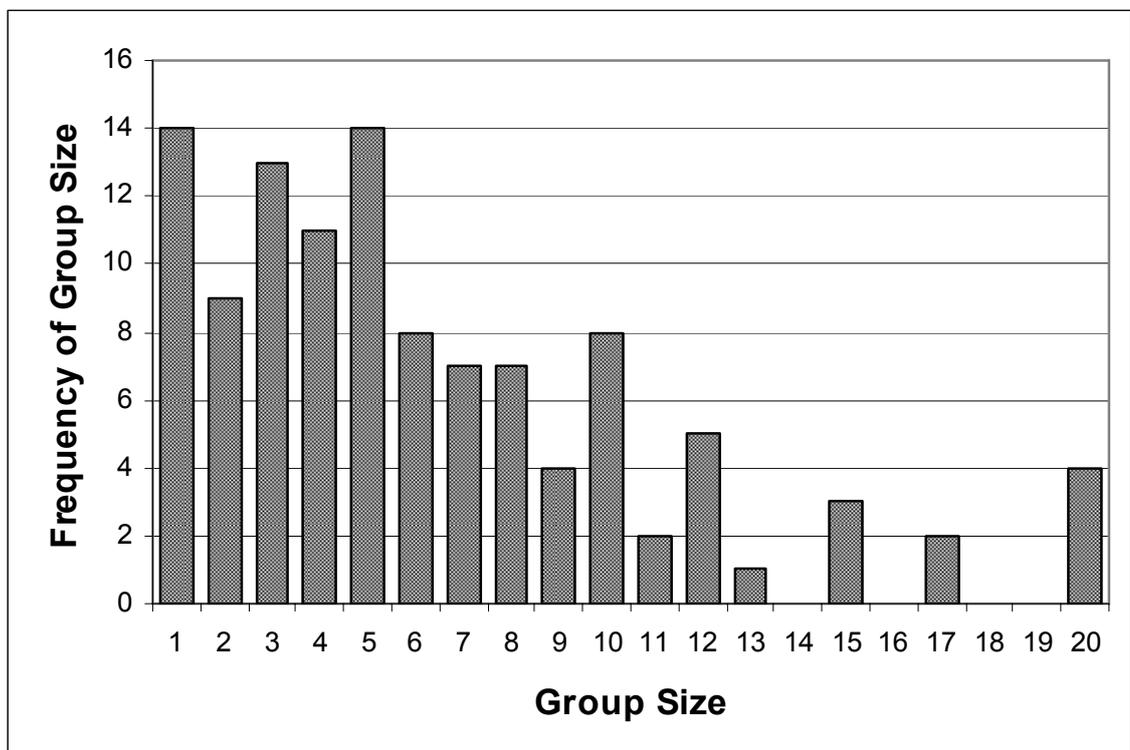
were made with those from phenology transects using the Mann-Whitney *U*-test. Species identifications for sleeping trees were also made using the same methods laid out in chapter 4.

## Results

### *Group size and composition*

#### **Group size**

Based on 112 encounters at the Camp 6 study site with reasonable group number estimates, mean group size was  $6.32 \pm 4.65$  individuals. The range was large, up to 20 individuals with a median number of 5. Data from WCS surveys returned a slightly higher mean group size ( $7.64 \pm 6.02$ ), with a range of 1 to 26, although median values were not significantly different between data sets ( $U = 4420$ ,  $p = 0.209$ ,  $n_{\text{Camp6}} = 112$ ,  $n_{\text{SBCA}} = 88$ , ns). With data sets combined, mean group size was  $6.90 (\pm 5.33)$  individuals or  $7.52 (\pm 5.22)$  if lone individuals are excluded. Figures 6-2 through 6-4 show the frequency distribution of the number of individuals per group for both data sets individually and combined.



**Figure 6-2** Frequency distribution of estimated group sizes from Camp 6 ( $n = 112$ ).

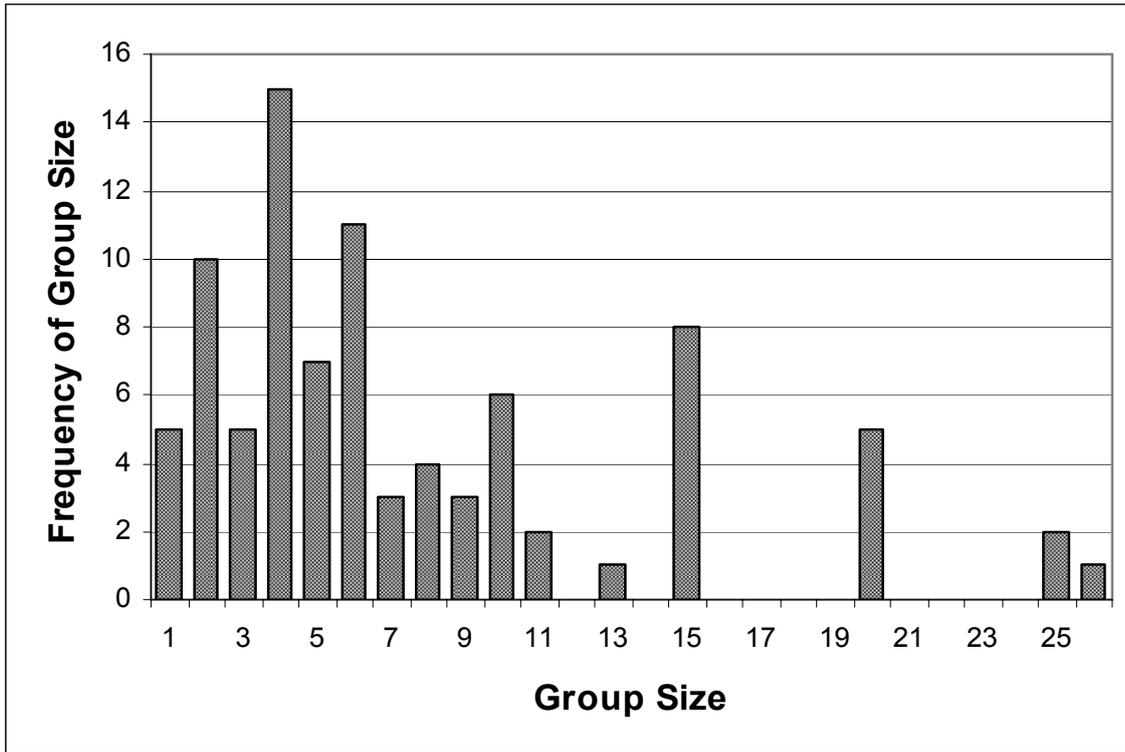


Figure 6-3 Frequency distribution of estimated group sizes from SBCA core area ( $n = 88$ ).

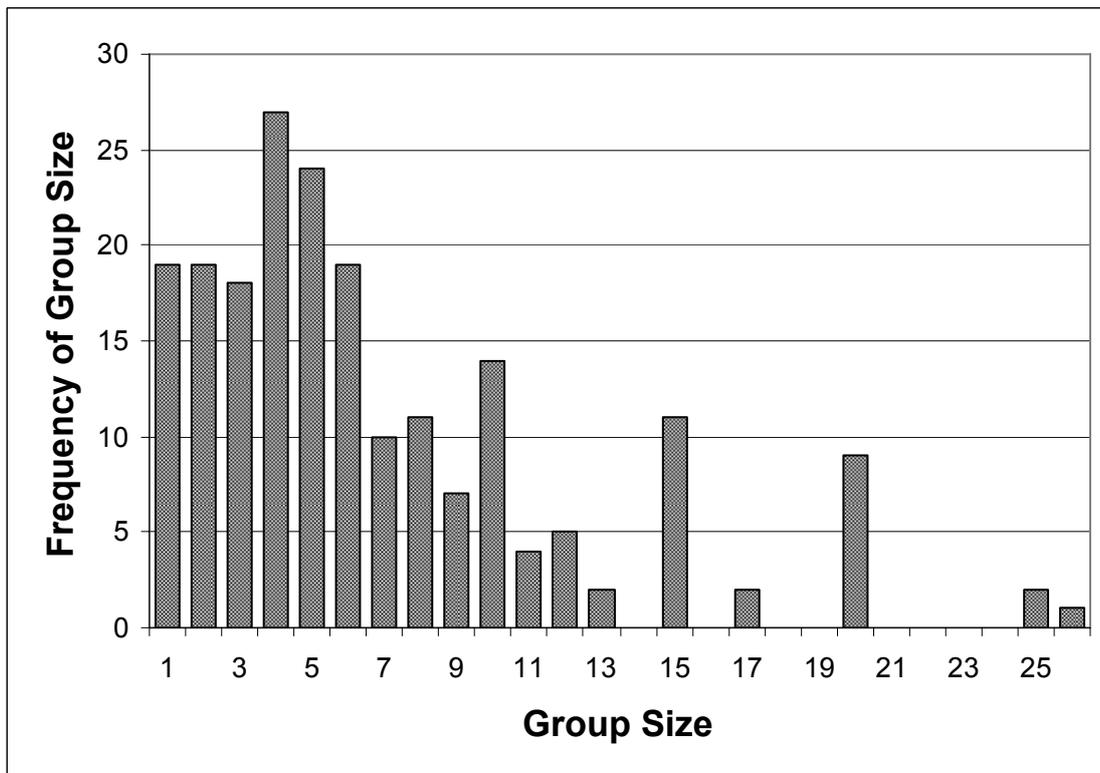


Figure 6-4 Frequency distribution of estimated group sizes from Camp 6 and SBCA core area combined ( $n = 200$ ).

### **Breeding group composition**

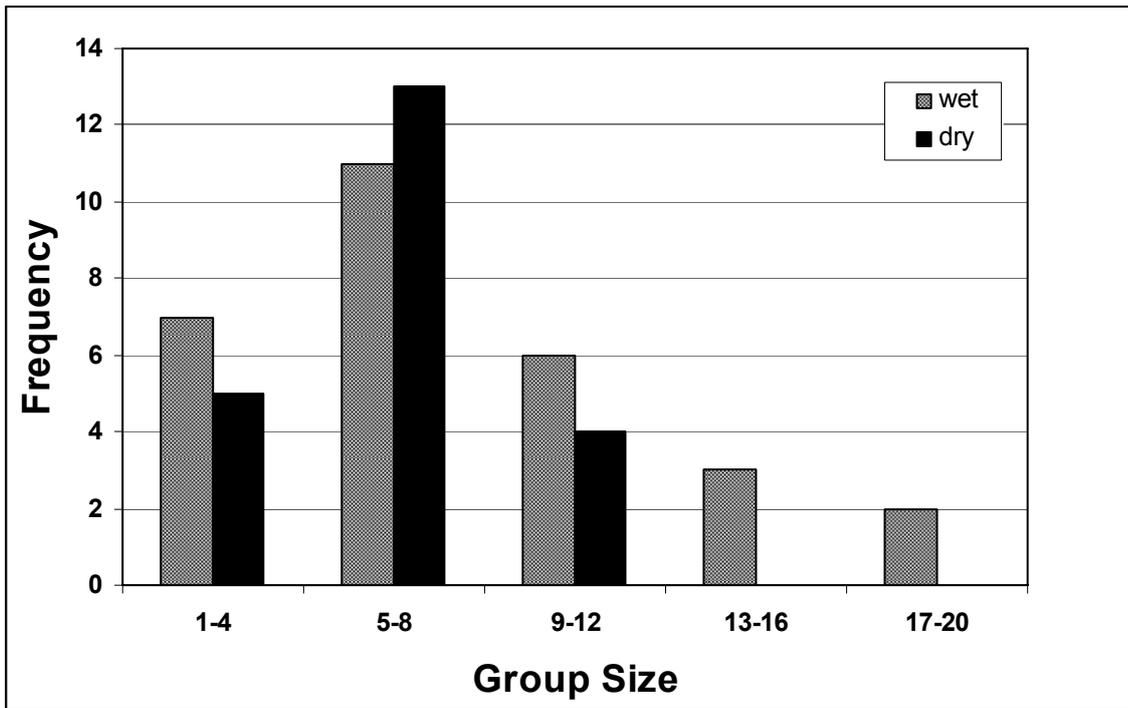
Data on breeding group composition were taken wholly from the Camp 6 data set as WCS data did not include age/sex classes. Of all encounters with douc groups at the site, there were only 21 instances where a full group count and age/sex class evaluation was possible on groups that contained both adult males and females. Groups for which this was achieved were generally smaller than average size presented above ( $\bar{x} = 5.48 \pm 2.14$ ) and so may not be wholly representative. Instead it may reflect the relative ease of getting confident group size estimates on smaller groups. The adult male:female sex ratio in these groups was 1:2.09. Instances of more than one adult male being recorded in a group were very rare. In the data set of groups with age/sex class fully identified ( $n = 21$ ), there was only one group with two males and this was the largest group in this data set, with 11 individuals. In the data set of groups with incomplete age/sex data only one other instance of two males in a group was recorded. The ratio of immatures to adults was also calculated from the same data set and returned a value of 1:0.63.

### **Unmated males**

Unmated males either ranged as lone individuals or came together to form bachelor groups. Solitary males were commonly encountered throughout the study period at Camp 6, and were commonly reported in WCS data for SBCA also. Only one bachelor group was encountered at the camp 6 study site during the study, although it was seen on two occasions within a few days of each other. This group comprised approximately 17 individuals composed of juvenile, subadult and adult males. Of six clearly observed, apparently full size, adult males, only one had all secondary sex characteristics, i.e. long chin whiskers, red penis and blue testicles. One more individual had a penis which was only  $\frac{3}{4}$  red, with the tip remaining 'skin' colour (pinkish beige) towards the tip. The remainder had only 'skin' colour penises as found among subadults. At least 2 subadults and 3 juveniles were also in the group.

### **Seasonality and group size**

Data from 51 sightings of douc groups from Camp 6 were available for analysis after removal of lone individuals, counts with low confidence and multiple counts of the same groups. Each observation was categorised as either from the wet season (May – October) or the dry season (November – April). Group size in the wet season ( $\bar{x} = 8.41 \pm 4.51$ ) was larger than that in the dry season ( $\bar{x} = 5.95 \pm 2.79$ ) and this reached significant levels ( $U = 211.50, p < 0.05, n_{\text{wet}} = 29, n_{\text{dry}} = 22$ ).



**Figure 6-5** Histogram of group sizes in the wet ( $n = 29$ ) and dry seasons ( $n = 22$ ).

### Habitat and group size

Group size difference between different habitat types was tested using WCS data from across the SBCA. After removal of lone individuals and incomplete records, data from 80 sightings of douc groups were available for analysis. A 200 m and a 500 m buffer was made around each observation locality using a GIS, and the area of four forest types—evergreen, semi-evergreen, deciduous and other—calculated. Amount of each forest type within that radius was determined using the JICA (2003) data set. The radius of 200 m and 500 m around each observation location was used as an estimator of ranging behaviour in the species and corresponds to areas of 12.56 ha and 78.54 ha respectively.

No significant correlation was found between habitat types and douc group size for either the 200 m or the 500 m radius. This may be because the buffers do not accurately represent areas the doucs are exploiting. For example, groups detected in the transition between evergreen and deciduous forest may not be using the deciduous element of the forest, however this will be included in analysis.

In order to further test the relationship between habitat type and group size, a student's *t*-test was performed on groups that were found in either homogenous evergreen or deciduous forest within the 500 m buffer. The rationale for this is that groups within this

area should be largely resident within that forest type. Although sample size was small for groups found in deciduous forest alone, the test returned a significant difference in group size between the two extreme habitat types ( $t = 3.723$ ,  $p = 0.002$ ,  $n_{\text{evergreen}} = 41$ ,  $n_{\text{deciduous}} = 4$ ), with mean group size values of 8.73 ( $\pm 6.24$ ) and 4.00 ( $\pm 1.63$ ) for evergreen and deciduous forest respectively.

### Habitat and group density

Encounter rates for doucs were calculated for each of WCS' 14 transects within the SBCA across three years (2003-2005). Mean encounter rate across all transects and years was 0.26 groups/km. Mean encounter rates from transects from this period ranged from 0.00 groups/km on transect 14, a quite disturbed area dominated by deciduous forest, to 0.68 groups/km on transect four, located wholly in evergreen forest. The highest encounter rate for any walk on any transect was 2.5 groups/km, which was on transect five in evergreen forest. Encounter rates for other primate species were considerably lower than those of doucs (see Table 6-1).

Species	Encounter Rate
<i>Pygathrix nigripes</i>	0.260 groups/km
<i>Macaca leonina</i>	0.085/groups/km
<i>Macaca fascicularis</i>	0.017 groups/km
<i>Macaca arctoides</i>	0.015 groups/km
<i>Trachypithecus margarita</i>	0.018 groups/km
<i>Nomascus gabriellae</i>	0.015 groups/km

**Table 6-1** Primate encounter rates on all transects, 2003-2005

Encounter rates were correlated with percentage of forest cover of different habitat types within 50 m of transect lines (see Table 6-2). Higher encounter rates were significantly positively correlated with the percentage of evergreen forest cover on transects and negatively correlated with degree of deciduousness. No correlation between percentage semi-evergreen forest and encounter rate was found, as might be expected, based on its intermediate nature.

	Evergreen	Semi-Evergreen	Deciduous
Pearson Correlation	0.561	-0.114	-0.605
Significance (2-tailed)	0.036*	0.699	0.022*
<i>n</i>	14	14	14

**Table 6-2** Significance values for Pearson product-moment correlation coefficient test of habitat type and encounter rates of black-shanked doucs.  
\* represents significant values at  $p < 0.05$ .

### Group cohesion

In most observed instances, females, often with infants, were seen to lead OMUs when travelling between areas. The adult male's position was either in the middle of the group or at the rear. OMUs would travel cohesively in single file along arboreal paths, with all individuals usually passing through a point within a few minutes.

When feeding, individuals of OMUs would feed in the same tree if it was relatively large and had a large amount of a preferred resource. More generally, however, individuals would feed over a larger area, usually within a 50 m diameter depending on the size of the group. Bands consisting of multiple OMUs cover much larger areas of 100 m diameter or more, still apparently forming cohesive OMUs within that area. There were no apparent sub-groupings within OMUs during general activities excepting infants and younger juveniles staying in close proximity to mothers.

Cohesion of groups when they were disturbed by the observers was variable and appeared to depend upon the distance between the observer and the group. When doucs spotted observers from a distance, approximately  $> 40$  m, adult males would usually vocalise to warn other members of the group and would sometimes display with fast and violent travel bouts in view while the rest of the group moved off. Responses of other age/sex classes were more variable, with individuals either alarm calling or fleeing without warning others in the group. At times it was possible to continue watching the remaining part of the group, although they were usually more vigilant post disturbance.

When researchers were observed at closer distances, doucs would often hide at the top of the canopy, or in dense lianas if available, rather than flee. Because individuals were sometimes spread out, this could result in the group being fragmented, with some animals fleeing while others hid, often for hours if the observer was suspected to be still

in the area. When OMUs did flee they would move off in the same general direction although not necessarily following the same arboreal pathways. In contrast, when bands were disturbed they would scatter, with OMU components apparently moving off cohesively.

## ***Ranging behaviour***

### **Day ranges**

Little information on ranging behaviour was available for analysis due to lack of individual recognition and short contact times (see Chapter 3). The only data that come close to a full day follow are from an OMU of seven individuals which began at 7:43 am and finished at 15:25 pm, a total of seven hours and 42 minutes. During that time, eight different UTM locations were marked and the distances between them calculated, for a total of 330 m travelled (see Table 6-3), or an average of 42.9 m/hour. If this is extrapolated to the whole activity period of approximately 12 hours, based on hours of activity during the day, as detailed in Chapter 5, then total day range distance would be approximately 514 m.

<b>Location</b>	<b>Leg distance (m)</b>	<b>Summed distance (m)</b>
1	0	0
2	29	29
3	15	44
4	29	73
5	80	153
6	58	211
7	61	272
8	58	330

**Table 6-3** Details of ranging behaviour of one group on 1st August 2004.

A mean hourly ranging distance was also calculated based on all encounters which returned more than one locational datum. Total time during each observation was divided by total distance travelled to arrive at an hourly average. From 1223 samples over 43.28 observational hours, and 20 discrete observations a mean of 78.61 ( $\pm$  66.58) m travelled per hour over the entire activity period was calculated. Based on a potential

activity period of 12 hours, from 6 am until 6 pm, this would give a day range of 943 m per day.

### **Home range**

As with day range, very little information on home range is available due to lack of individual recognition and habituation and fission/fusion behaviour. One group of five individuals, called CG1, was located on eight occasions, which were insufficient for constructing a reliable home range estimate using minimum convex polygon size. However, due to the paucity of home range data in the genus, it can be noted here that the minimum convex polygon size estimate was 20.1 ha, and that the maximum distance between any two points was 1,070 m.

### **Sleeping sites**

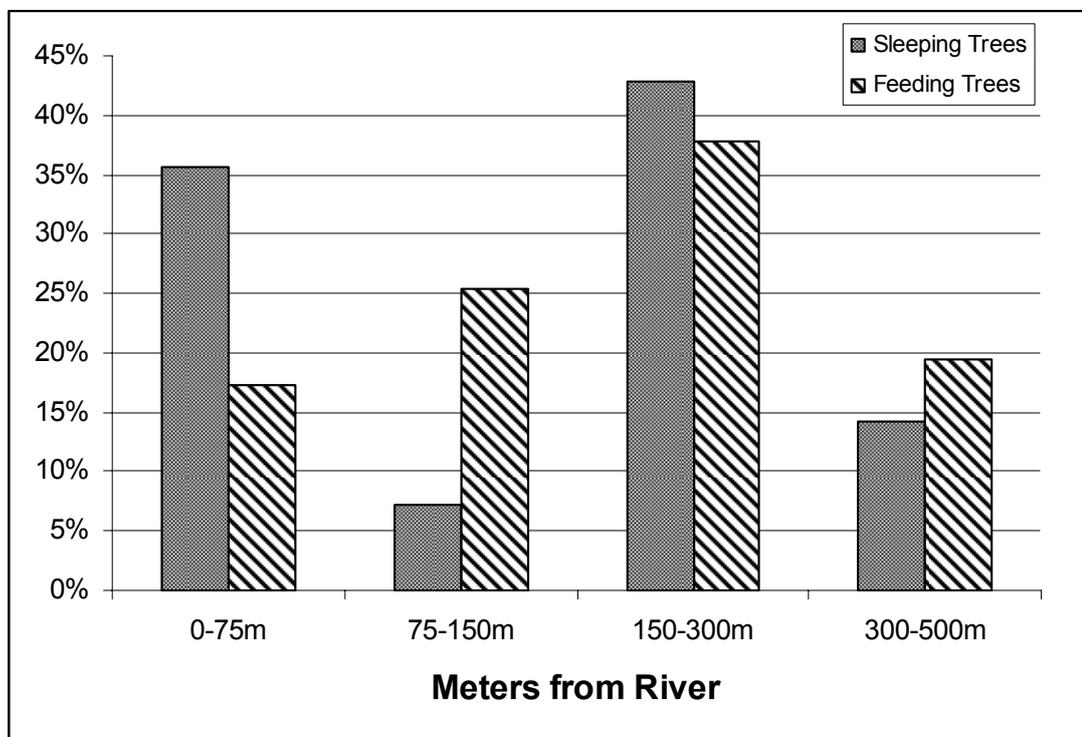
In total, 14 sleeping sites were identified during the course of the study, all of which were from direct observation of doucs settling down for the evening. No sleeping site was seen to be used more than once. The location of sleeping sites seems to be preferentially located near rivers although sample size is small. To provide some measure of preference for riverine areas for sleeping sites, the distance of sleeping sites from rivers was calculated using a GIS, and compared with the distribution of feeding trees relative to rivers. Survey effort is identical for these two factors, although comparisons do not account for non-random distribution of feeding trees.

Although Figure 6-6 suggests that a relatively larger fraction of sleeping trees were located close to rivers than feeding trees, this did not reach significant values ( $U = 1167.5$ ,  $p = 0.50$ ,  $n_{\text{sleeptree}} = 14$ ,  $n_{\text{feedingtree}} = 186$ , Mann-Whitney  $U$ -test).

Information was also collected where possible on the species, height and DBH of sleeping trees (see Table 6-4). Of the six measured and identified sleeping trees, all were species that the doucs fed from at some time during the study. Further, of the five species, all except one, *Ficus* sp., were in the top five preferred feeding tree species (see Chapter 7).

Species	Family	Height (m)	DBH (cm)
<i>Aflexia xylocarpa</i>	Fabaceae	17	56.37
<i>Sindora siamensis</i>	Fabaceae	21	123.57
<i>Ficus</i> sp.	Moraceae	19	105.00
<i>Irvingia malayana</i>	Irvingiaceae	20	125.48
<i>Irvingia malayana</i>	Irvingiaceae	26	164.97
<i>Peltophorum cf. dasyrrhachis</i>	Fabaceae	22	31.85

**Table 6-4** Sleeping tree species, height and DBH.



**Figure 6-6** Percentage of sleeping ( $n = 14$ ) and feeding ( $n = 186$ ) trees within distance categories from nearest river.

Mean height for sleeping trees was 20.83 ( $\pm 3.06$ ) m, and mean DBH was 101.16 ( $\pm 48.95$ ) cm. Sleeping trees' heights were not significantly larger than those from phenology Transects 1 and 2 combined, although it approached significance ( $U = 673$ ,  $p = 0.07$ ,  $n_{\text{sleeptree}} = 6$ ,  $n_{\text{transects}} = 394$ , Mann-Whitney  $U$ -test) while DBHs were significantly larger for sleeping trees than phenology transect trees ( $U = 134$ ,  $p < 0.001$ ,  $n_{\text{sleeptree}} = 6$ ,  $n_{\text{transects}} = 397$ , Mann-Whitney  $U$ -test). Doucs would usually sleep in the upper canopy of sleeping trees, with several individuals usually in one tree.

## Discussion

### *Group size and composition*

#### **Group size**

The figures presented here for douc group size represent the most comprehensive yet published, with group estimates based on 200 encounters. Group size was found to average approximately 6.9 individuals, with groups as large as 26 individuals encountered. The fairly large complement of sightings of lone individuals ( $n = 19$ ) reduced the average group size. When these are removed average group size is approximately 7.5 individuals. Little information is available on group sizes on the species from other locations; those that are available are presented in the following paragraphs.

In Cat Tien National Park, Vietnam, there are frequent observations of groups of black-shanked doucs with group sizes ranging from two to seven animals, although there have been several observations of groups of 10-16 individuals (Nadler *et al.*, 2003). Ironically, the best documented group sizes for the species come from Yok Don National Park, Vietnam, with 16 records (Ngo Van Tri, 2003a, Ngo Van Tri, 2003b, Nguyen Hao Hoa and Ben Rawson, unpublished data). This area has very little available habitat, located mainly on Yok Don Mountain, and apparently has only a very small and localised population of doucs (pers. obs). Group sizes there were  $5.16 \pm 1.50$  animals in the dry season and  $6.44 \pm 4.33$  in the wet season.

Three black-shank groups on the Di Linh plateau, Vietnam, numbered 10-15, 10 and 20 individuals (Eames and Robson, 1993). Other surveys from the area have reported two groups of 15-20 individuals (Vu Ngoc Thanh pers. comm. in Nadler *et al.*, 2003) and one group of 22 individuals (Pham Nhat pers. comm. in Nadler *et al.*, 2003). On The Da Lat plateau, Eames and Nguyen Cu (1994) reported a group of two individuals and a group of 18 individuals, while in Kong Cha Rang group size was about 40 individuals (Lippold, 1995).

Groups of 45 and two (Ha Thang Long, 2002), six, 10 and 30 (Hoang Minh Duc and Ly Ngoc Sam, 2005) individuals had originally been reported in Nui Chua National Park, Vietnam. More detailed studies there showed an average group size at the site of 13.06 ( $\pm 9.60$ ), or 8.8 ( $\pm 3.00$ ) for OMUs (Hoang Minh Duc, 2007). This is slightly higher

than that found in Phuoc Binh National Park at 10.13 ( $\pm$  5.03) or 7.7 ( $\pm$  3.20) for OMUs (Hoang Minh Duc, 2007).

In Cambodia published information is more limited than for Vietnam. Sightings of three groups in north-eastern Mondulhiri Province returned group size estimates of between two and 20 individuals per group (Long, 2000).

While the information presented here from other areas within the species' distribution range is fragmentary and usually based on rounded estimates, it generally concurs with the *range* in group size found in SBCA. However, *mean* group size from other published data is significantly larger than the average group size presented here. This raises the question as to why group size at SBCA seems low. Four hypotheses are presented here.

Firstly, it is possible that group sizes at SBCA are smaller than at other sites because the habitat here is suboptimal. It has been posited that a correlation exists between group size in doucs and habitat disturbance, with more disturbed habitats supporting smaller group sizes (Lippold, 1998) as detailed in the ecological-constraints model (e.g. Chapman *et al.*, 1995, Gillespie and Chapman, 2001). Levels of habitat disturbance have not been assessed during this study. However, limited botanical work in the SBCA suggests that while many areas have been logged to some degree in the recent past (Walston *et al.*, 2001, Zimmermann and Clements, 2002), most recently commercially by Samling International Ltd (see Chapter 2 and Chapter 4 for more detail), the forest is generally little disturbed and still retains a good proportion of tall trees and good canopy cover (Walston *et al.*, 2001, Evans *et al.*, 2003).

A second potential hypothesis, also pertaining to sub-optimal habitat, is that maximum group size is restricted by habitat type. Although it seems that evergreen forest can support larger group sizes than the very marginal dry deciduous dipterocarp forest (see "Does habitat and season affect group size and density?" below) those numbers are still very low, averaging less than nine individuals in the SBCA. This suggests that it is not the habitat type *per se* within the SBCA which is responsible for returning numbers generally lower than those found in the literature.

Thirdly, hunting pressure would also be assumed to reduce group size. However, hunting of doucs within SBCA is currently minimal with only one record between 2003 and 2005 to my knowledge. If hunting was common before the study it probably

declined after 1998 when a national gun confiscation program was initiated. The European Union Assistance on Curbing Small Arms and Light Weapons in Cambodia, and other gun confiscation programs, removed 138,154 guns between 1999 and 2004 (EU-ASAC, 2004). Since then most hunting within the area has involved snaring or hunting with guns at night, neither of which would be thought to place pressure on diurnal primates (Rawson *et al.*, in press).

Pressure at the site may have been greater in the past; however, as Long (2000) noted, black-shanked doucs are specifically targeted throughout their range for use as food, traditional medicine and as pets. There has been an upward trend in the frequency of encounters with doucs since protection work started at the site (Pollard *et al.*, 2007), although this represents increased numbers of groups seen, not necessarily an increase in group size. This may represent additional recruitment though it may also represent increased skill of observers and/or reduced flushing distance due to increased protection at the site.

Finally, it may be that as all previous group size estimates come from general surveys, and not from long term observations (with the exception of the work of Hoang Minh Duc (2007)), that the subtleties of group dynamics in the species and possibly the genus have not been fully appreciated. This hypothesis is explored in more detail below.

### **Group composition**

The majority of work on group structure in doucs has been done by Lois Lippold, who has worked on red-shanked doucs since the mid 1970s. Her early observations in Son Tra Nature Reserve suggested that red-shanked doucs form both OMUs and MMUs (Lippold, 1977), which was reinforced by Gochfeld (1974) at the same site. More recently, however, survey results by Lippold (1998) have returned only MMUs from surveys within several protected areas (see Table 6-5). Based on this work, doucs' basic organisational structure is often listed as the MMU (e.g. Nadler *et al.*, 2003).

These figures come from relatively short term surveys, not long term ecological studies, and include data on group composition in red-shanked doucs (*P. nemaus*) only, not black-shanked doucs. As Kirkpatrick (1998) points out, *Nasalis larvatus* groups were originally characterised as MMUs based on short-term studies, but that with longer, more intensive studies, it was determined that in fact the basic social structure was the OMU. This raises the question, have doucs been classified as forming MMUs because

of the brevity of studies which have overlooked a more complex social structure involving fission-fusion of OMU's?

Long (2000) hinted that OMUs might be the modal form of social organisation in black-shanked doucs, reporting that groups of three to eight individuals were sometimes observed, followed quickly by another group of similar size. Captive bred doucs are preferably housed in OMUs (Hollihn, 1973, Lippold, 1989), as males will fight when a female is so much as sighted (U. Streicher, pers. comm.). Indeed, OMUs are the typical social grouping in Asian colobines (Yeager and Kool, 2000) and it has been hypothesised that this could be the case in the genus *Pygathrix*, based on similar group structures in the other closely related odd-nosed colobines (Yeager and Kirkpatrick, 1998, Kirkpatrick, 1998). Newly emerging field data have also suggested that *Pygathrix* has a basic grouping structure of OMUs (Hoang Minh Duc, 2007). In fact, all odd-nosed colobines (except *Simias concolor*) show a pattern of OMUs more or less loosely coming together to form larger bands of individuals.

Site	Species	Group Size	OMU	MMU	Reference
This study	<i>P. nigripes</i>	7.52 ( $\pm$ 5.22)	X	X	This study
Nui Chua NP	<i>P. nigripes</i>	13.06 ( $\pm$ 9.60)	X	X	(Hoang Minh Duc, 2007)
Phuoc Binh NP	<i>P. nigripes</i>	10.13 ( $\pm$ 5.03)	X	X	(Hoang Minh Duc, 2007)
Son Tra NR	<i>P. nemaesus</i>	6		X	(Lippold and Vu Ngoc Thanh, 1998)
Son Tra NR	<i>P. nemaesus</i>	17		X	(Lippold and Vu Ngoc Thanh, 1998)
Pu Mat NP	<i>P. nemaesus</i>	25-35		X	(Lippold, 1998)
Bach Ma NP	<i>P. nemaesus</i>	4-5		X	(Lippold, 1995)
Bach Ma NP	<i>P. nemaesus</i>	20-25		X	(Lippold, 1995)
Son Tra NR	<i>P. nemaesus</i>	8	X		(Lippold, 1977)
Son Tra NR	<i>P. nemaesus</i>	9	X		(Lippold, 1977)
Son Tra NR	<i>P. nemaesus</i>	11		X	(Lippold, 1977)
Son Tra NR	<i>P. nemaesus</i>	5	X		(Gochfeld, 1974)
Son Tra NR	<i>P. nemaesus</i>	7		X	(Gochfeld, 1974)

**Table 6-5** Literature summary of genus *Pygathrix* group size and composition

All *Rhinopithecus* species appear to display a one-male multi-female core breeding unit (OMUs). Dong Thanh Hai's (2006) long-term observations on the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*) at Tat Ke sector of Na Hang Nature Reserve, and in Khau Ca Tonkin Snub-nosed Monkey Conservation Area, suggest that the core grouping pattern of the species is OMUs, but that these stable breeding groups may coalesce into larger bands to sleep, feed or travel, as originally suggested by Boonratana and Le Xuan Canh (1998).

The same general group structure appears to apply to all the Chinese representatives of the genus, although bands seem to be larger, at least in current times, than those of *R. avunculus*. *R. brelichi* forms OMUs averaging 6.1 individuals, with these coalescing to form larger bands of  $\geq 400$  individuals (Bleisch *et al.*, 1993, Bleisch and Xie Jiahua, 1998). *R. bieti* and *R. roxellana* also show this pattern with breeding groups coming together to form large bands, although documented band size may be smaller than in *R. brelichi* (Kirkpatrick *et al.*, 1998, Ren Renmei *et al.*, 1998).

*Nasalis larvatus* also forms OMUs (Yeager, 1995) with an average group size of nine individuals at one study site (Bennett and Sebastian, 1988), and 17 and 14.6 at two other sites (Boonratana, 1993). These OMUs generally came together at night along rivers to sleep and often travelled together during the day suggesting a higher level of organisation (Bennett and Sebastian, 1988, Boonratana, 1993, Yeager, 1995) similar to bands in the Chinese *Rhinopithecus* species, although perhaps not as cohesive.

Observations made during this study, supported by a concurrent study in Vietnam (Hoang Minh Duc, 2007), seem to confirm that this general pattern is also found among black-shanked doucs. That is, the core group formation is small OMUs consisting of a single male, associated females and their offspring. These are presumably breeding groups. These OMUs may come together to form larger congregations, possibly up to 50 individuals, although the largest recorded group from SBCA was 26. These super groups, or bands, might spread out over 100 m diameter and superficially appear to be one "group". During observations, however, if there was sufficient observation time, OMUs could generally be discriminated from the larger band, based on individual's travel trajectories and/or cohesiveness and proximity. For example, when groups are startled, OMUs may move off in different directions.

The basis of any relationship between these OMUs that coalesce into bands is unknown. As individual recognition was not achieved, it is unknown whether these bands consistently form from the same OMUs or not. It is likely that, over longer timeframes than OMUs were observed, transfers between OMUs occur. It appears that the low levels of inter-OMU aggression (see Chapter 5) permit the aggregation of OMUs into these large bands. Further research into this phenomenon is required for full clarification. It should also be kept in mind that all douc species may not have the same group formation as that presented here; and that the MMU may be the predominant social structure in, for example, red-shanked doucs (Lippold, 1977, Lippold, 1998). Based on my limited experience observing grey-shanked doucs (*P. cinerea*) in Que Phuoc district, Quang Nam Province Vietnam, this species has a similar grouping pattern to that of black-shanked doucs.

Male to female sex ratios found during this study mirror those found for other studied *Pygathrix* populations (Lippold, 1977, Hoang Minh Duc, 2007), with one male for approximately every two females (see Table 6-6). In primates in general, sex ratios at birth are 50:50, although this may be impacted by differential mortality during maturation (Dunbar, 1987). Female positive bias in this case may be related to the low incidence of observations of AMU, skewing figures, although higher levels of juvenile and adult mortality in males has also been posited as a possible explanation (Hoang Minh Duc, 2007). No additional demographic data are available to tease apart these potential hypotheses. Adult to immature ratios were found to be within the range of other odd-nosed colobine species (Table 6-6).

### **Unmated males**

Males outside the bisexual groups were either solitary or in all male groups (AMUs). Lone males were seen quite regularly during the study and in other locations where the species is found (Hoang Minh Duc, 2007). Lone males are apparently quite rare in Asian colobines who tend to form bachelor groups (Newton and Dunbar, 1994), although both solitary males and all male groups are also seen in *Nasalis larvatus* (Bennett and Sebastian, 1988, Boonratana, 1993).

Conversely, only one bachelor group was seen in the current study, and seen only on two occasions within a few days of each other. This group was large, with at least 17 members, which seems quite large compared to most other odd-nosed colobines. While *N. larvatus* AMUs have been recorded to be as large as 16 individuals (Bennett and

Sebastian, 1988), this is not the case among the *Rhinopithecus* species. AMUs are commonly quite small in these species: two to five individuals in *R. brelichii* (Bleisch *et al.*, 1993), four to seven in *R. roxellana* (although these would aggregate to groups of up to 26 under certain circumstances) (Ren Renmei *et al.*, 1998) and similar sizes in *R. bieti* (Kirkpatrick *et al.*, 1998). In *R. avunculus* bachelor groups may be larger, with two reported groups having 12 and eight individuals (Boonratana and Le Xuan Canh, 1998), although more recent observations found smaller bachelor groups of five and four individuals (Dong Thanh Hai, pers. comm.), although high hunting pressure may be skewing these figures.

Species	Male:Female	Adult: Imm	Reference
<i>Pythagrix nigripes</i>	1:2.09	1:0.63	This study
<i>P. nigripes</i> Phuoc Binh NP	1:2.09	Not given	(Hoang Minh Duc, 2007)
<i>P. nigripes</i> Nui Chua NP	1:1.78	Not given	(Hoang Minh Duc, 2007)
<i>P. nemaesus</i>	1:2.7	1:0.9	(Lippold, 1977)
<i>Rhinopithecus bieti</i>	1:3.1	1:1	(Kirkpatrick <i>et al.</i> , 1998)
<i>R. brelichii</i>	1:2.2	1:0.9	(Bleisch <i>et al.</i> , 1993, Bleisch and Xie Jiahua, 1998)
<i>R. roxellana</i>	1:4.4		(Ren Renmei <i>et al.</i> , 1998)
<i>Nasalis larvatus</i>	1:3.8	1:0.9	(Bennett and Sebastian, 1988)
<i>N. larvatus</i>	1:3.6	1:0.8	(Yeager, 1990)
<i>N. larvatus</i>	1:7.5	1:1.1	(Boonratana, 1993)
<i>Simias concolor</i>	1:1.7	1:0.8	(Watanabe, 1981)
<i>S. concolor</i>	1:1.8	1:0.4	(Tenaza and Fuentes, 1995)

**Table 6-6** Male:Female and Adult:Immature ratios in odd-nosed colobine species.

The single AMU of black-shanked doucs observed during this study was composed of all age classes except for infants, although only one individual was seen to have all secondary sexual characteristics, despite the fact that at least six individuals seemed to be fully grown. Other sightings of AMUs in the species have tended to suggest very few fully mature males being present (Hoang Minh Duc, 2007). Further, in a brief field study of *Rhinopithecus avunculus*, two AMUs were seen, totalling 20 individuals, but

again there was only one fully adult male in each group (Boonratana and Le Xuan Canh, 1998). Other observations for the species suggest that such groups are composed mainly of subadults and juveniles (Dong Thanh Hai, pers. comm.). Data from the Chinese *Rhinopithecus* species are less clear, with AMUs composed of adults, subadults and juveniles, although information on numbers of each and relative degree of secondary sexual characteristics in these groups is lacking (Bleisch and Xie Jiahua, 1998, Ren Renmei *et al.*, 1998, Kirkpatrick *et al.*, 1998). In *N. larvatus* data from two AMUs showed that each contained only one subadult male, which was of adult size but without fully developed secondary sexual characteristics, plus several juveniles (Bennett and Sebastian, 1988). In captivity, developmental suppression of subdominant males by dominant males has been noted for this species also, with development resuming and adulthood attained rapidly with the removal of the dominant individual (Hollihn, 1973). While developmental suppression of subadult males by dominant males can not be demonstrated in doucs, it is an intriguing possibility that this characteristic may be common to all the odd-nosed colobines.

### **Does habitat and season affect group size and density?**

Theory suggests that group size is determined by the costs and benefits incurred and accrued for each individual within the group (Wrangham *et al.*, 1993, Kappeler and Van Schaik, 2002). That is, each individual makes decisions about what value being part of a group has for them and stays or leaves accordingly. One of the most pressing concerns for any individual living in a group is being able to access sufficient food. The major limiting factors in acquiring sufficient nutrition are the relative abundance of food resources within the environment and the degree of competition that other members of the group present, either directly or indirectly (Wrangham *et al.*, 1993, Gillespie and Chapman, 2001, Kappeler and Van Schaik, 2002). As group size increases so too do the costs to the individual for remaining in that group; competition over resources becomes fiercer and day ranges may need to be increased to satisfy dietary requirements. Upper limits on group size may therefore be limited by these increasing costs (Janson and Goldsmith, 1995, Gillespie and Chapman, 2001, Kappeler and Van Schaik, 2002, Chapman and Pavelka, 2005)

It has been argued that food may not be a significant limiting factor in colobine species (Yeager and Kirkpatrick, 1998), as they are typified as leaf-eaters and leaves are obviously abundant within tropical forest settings. Milton (1984), however, demonstrated that leaf eating primates are more selective feeders than initially assumed,

preferentially consuming species with low fibre to protein ratios. Data provided in Chapter 7 of this thesis, and below, demonstrate that black-shanked doucs are very selective feeders, which will limit group size and density for the species.

There are three pertinent findings in this study related to group size and density as it relates to habitat and resource availability. First, group density is correlated with evergreen habitat availability; the WCS data showed that encounter rate on transects was significantly lower in areas containing dry deciduous dipterocarp forest types. This is not overly surprising. This latter forest type is almost certainly unsuitable for doucs, with very low species diversity and large canopy gaps. While doucs have been seen moving through this forest type (Pollard *et al.*, 2007, pers. obs.), it is likely they may only be en route to more evergreen areas within the habitat mosaic.

Second, there is evidence, based on the WCS data set, that group size in evergreen forest is larger than in areas containing a large amount of dry deciduous forest. That is, poor habitat quality may limit the upper limit of group size. There is therefore some suggestion that the ecological-constraints model may be appropriately applied here though this can not be confirmed as vital ranging data are lacking in this study. Results showed no correlation between semi-evergreen forest and encounter rate or group size, however, which may be related to the variable nature of semi-evergreen forest. Unfortunately, the JICA (2003) data set does not distinguish between various species assemblages of semi-evergreen forest (Chapter 4). *Lagerstroemia* dominated forest type may be marginal habitat for doucs as has been suggested for yellow-cheeked crested gibbons (Rawson *et al.*, in press). As such, information regarding the appropriateness of this forest type for doucs is of importance as it may be a limiting factor in the distribution of doucs across their extent of occurrence. This topic is addressed in more detail in Chapter 7.

The third finding was that group size is significantly larger in the wet season than in the dry season. Again, this points to a trend in fission-fusion behaviours, with OMUs fusing more commonly during the wet season and remaining in core breeding groups during the dry. During the dry season, only 18% of observations involved groups of 10 or more individuals, whereas in the wet, it was 34%. The question is then, what is driving these patterns of fission and fusion?

While not definitive, various lines of evidence suggest that fusion in the wet season may be due to higher resource availability of preferred foods at this time. When we look at the availability of the top six most consumed tree species, which constitute almost 50% of feeding records, we can see that fruit abundance is higher in the wet season (May-October) (see Table 6-7). This abundance of preferred food items at this time may permit OMU's to forage together in larger bands, as in other primates showing fission-fusion group dynamics (Chapman *et al.*, 1995, Lehmann *et al.*, 2007).

Species	<i>n</i>	Evergreen Deciduous†	New Leaves	Flower	Fruit
<i>Irvingia malayana</i>	6	Evergreen	Feb-Mar	NU	Mar-Jun
<i>Azelia xylocarpa</i>	2	Evergreen	Jan-Apr	Feb-Mar	Apr-May
<i>Peltophorum cf. dasyrrhachis</i>	1	Deciduous	NU	NU	Apr-Aug*
<i>Anogeissus acuminata</i>	9	Deciduous	Apr-Jun	NU	Nov-Feb
<i>Syzygium</i> sp.	4	Evergreen	NU	NU	May
<i>Millettia</i> sp.	4	Evergreen	Nov-Feb	Feb	Mar-June

**Table 6-7** Six most preferred species and the monthly availability of utilised plant parts based on transect data.

NU = Not utilised.

\* The one individual on phenology transects was never seen to fruit, however data from feeding observations suggest it fruits from April – August.

Anecdotal evidence from Yok Don National Park supports this hypothesis. Group size of *P. nigripes* in Yok Don NP was suggested to be larger in the wet season than in the dry (Ngo Van Tri, 2003a, Ngo Van Tri, 2003b) although the author attributed this to ongoing hunting pressure which reduced group size between surveys (the wet season was the first survey). A short study has been conducted here on black-shanked doucs by Scientific and Technical staff of the National Park, which includes data on group size. Mean group size in the wet season (8.2 ( $\pm 7.70$ )) was larger than in the dry (6.19 ( $\pm 3.95$ )) although, the difference is not significant ( $U = 55.5$ ,  $p = 0.554$ ,  $n_{\text{wet}} = 10$ ,  $n_{\text{dry}} = 13$ ) probably due to the large variability in group size during the wet season (Nguyen Hao Hoa, unpub. data.).

Hoang Minh Duc's (2007) study of black-shanked doucs also found a seasonal difference in group size, with larger groups recorded in the wet season, although this did not reach significance. He discarded the hypothesis that resource abundance was driving

this apparent pattern in favour of a hypothesis that group size was tracking reproductive cycles. Theoretically, smaller groups would be associated with the mating season at these sites (June – September), with bands fissioning to allow males to defend mates more effectively (Hoang Minh Duc, 2007). Data presented did not support this assertion, with no significant differences found in group size between mating, breeding and intermediate “seasons”.

The findings presented here, which show larger group sizes in the wet season, run contrary to previous hypotheses concerning fission-fusion in doucs. Otto (2005) hypothesised that fission in doucs may be expected to occur during periods of low abundance of new leaf. The reasoning was that as mature leaves contain greater relative amounts of fibre and secondary compounds, in order to avoid negative effects animals would have to forage more widely and on a greater range of plant species. In other words, when new leaf patch sizes become small, bands would be expected to fission, with OMUs breaking off to forage separately to avoid competition.

Chapter 4 shows, contrary to this hypothesis, that new leaf availability at the site is chronically low during the wet season when fusion is occurring. While young leaves were a vital part of the diet of doucs at the site, comprising 24% of the overall diet, it appears that seeds comprise a considerably larger part of the diet and are preferred food items (Chapter 7). Young leaf is most likely a fall back resource when seeds are less available (e.g. Brugiere *et al.*, 2002). Logically, this being the case, it will be seed availability, not young leaf availability which determines fission-fusion behaviour. Referring to Table 6-7, four of the six preferred plant species exploited are targeted for seeds. While, it seems that resource availability, specifically seeds, may play a vital role in determining group movements and fission and fusion, more research needs to be done on this subject, particularly looking at the patchiness and seasonality of key resources identified during this study across habitat types.

### ***Ranging behaviour***

One of the limitations of this study was the failure to accurately document ranging behaviour in black-shanked doucs. Some preliminary numbers are presented based on poor data and should be interpreted with *extreme* caution. Estimates of day ranges based on hourly rates were presented based on two approaches as 514 m per day or 943 m per day. Both of these estimates have intrinsic problems, in that the first is based on only a limited period of the day and on only one follow, while the other has a large standard

deviation. These figures are presented here merely because there are no data in the literature, and so simply provide a broad baseline for future studies. The only other study of *Pygathrix* day ranges comes from Hoang Ming Duc (2007) who, based on 16 full day follows, found a range of day range distances between 658 m to 1666 m. No seasonal trends in ranging behaviour were found, probably due to small sample size.

Home range data presented here are also poor with the figure of 20.1 ha likely being a large underestimate. The only other data on home range in *Pygathrix* again come from Hoang Minh Duc's work on *P. nigripes*, which returned an average from three groups of 42.3 ha for minimum convex polygon methods and 47.5 ha based on grid-cell counts (Hoang Minh Duc, 2007). No data on home range overlap exist, but it is clear that it is considerable, with groups of different sizes and compositions found in the same area repeatedly.

In terms of sleeping tree use, the fact that animals travelled considerable amounts in the late afternoons (see Chapter 5) meant that observers were seldom able to maintain contact with groups to the point where they took to sleeping trees. Further, animals would occasionally seemingly select a site in the late afternoon, only to move off again at dusk, possibly a cryptic behaviour aimed at avoiding predation (Anderson, 1998). In all, sleeping sites were positively identified on only 14 occasions. There is some suggestion that sleeping site locations were preferentially located near rivers as has been suggested anecdotally in the past (Hoang Minh Duc and Ly Ngoc Sam, 2005). Other suggestive evidence for a preference to sleep near rivers from this study comes from the high levels of travel in the afternoons, as groups make their way from areas preferred for feeding to those preferred for sleeping. This is a pattern found among proboscis monkeys (*N. larvatus*), although it is very stereotyped in that species (Bennett and Sebastian, 1988). There was, however, no statistically significant evidence for a preference to sleep near rivers, which may be because of the small sample size. Sleeping trees were apparently chosen, at least partially, on the basis of their size, with trees with larger DBHs and heights selected preferentially. This use of large trees is likely related to predator avoidance. Sleeping trees may also be selected based on tree species as all sleeping trees were also found to be preferred food trees during the study.

## Summary

Observations throughout the study suggest that black-shanked douc individuals form four types of group. The basic unit appears to be the OMU, which consists of an adult male, associated females and their offspring. Extra males either range as lone individuals (unit 2) or form bachelor bands (unit 3). The fourth unit is the band, where multiple OMUs group together, more or less loosely, to form a large band reaching as many as 26 individuals from the SBCA, although anecdotal evidence suggests they may reach up to 50 individuals. To what extent some groupings interpreted here as bands are actually MMUs is unclear; this social grouping may also occur, although it appears to be relatively uncommon.

Group size was affected by season and habitat. Temporal variability in group size was detected, larger groups being found during the wet season than the dry season. This correlates with apparently higher resource abundance of preferred plant species; the link between what may be fusion of OMUs into bands at this time of year and resource abundance can only be hypothesised at this time. To fully understand the dynamics of fission and fusion in doucs, individual recognition and high quality data across months for both forest productivity and group size are required, the first of which is lacking in the current study. Group size also appears to be affected by habitat quality to some degree as does group density, with smaller groups found less frequently in less optimal habitat. The ecological-constraints model may possibly be applied to black-shanked doucs, and this remains a fertile topic for additional study.

## ***Feeding ecology***

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### **Introduction**

Colobines have traditionally been referred to as “leaf-eating monkeys”, but this moniker has, over the course of time, been shown to be less accurate than originally thought, as the diversity of feeding strategies the subfamily displays have become more thoroughly understood (Kirkpatrick, 2007). Colobines do of course have morphological adaptations that enable them to consume large quantities of leafy material, adaptations which separate them from the Cercopithecinae. These are most notably dental adaptations (Lucas and Teaford, 1994), large salivary glands (Kay and Davies, 1994) and the presence of a complex stomach and other physiological adaptations of the gastrointestinal tract which, together with symbiotic fermenting bacteria, aid in the effective digestion of plant material (Chivers, 1994). This ability to process plant materials and counter digestion inhibitors and toxins allows colobines access to plant resources not readily available to monogastric primates. It also probably facilitated an adaptive radiation of the Colobinae (Delson, 1994) and an avoidance of competition today with modern day Cercopithecinae with whom they are frequently sympatric.

The diversity of colobine diets is now well documented (see Table 7-7 for a summary of Asian colobine diets). Some species have been shown to have high proportions of leaves in their diet such as *Rhinopithecus brelichi* (Bleisch *et al.*, 1993, Bleisch and Xie Jiahua, 1998), *Presbytis hosei* (Rodman, 1978) and *Trachypithecus leucocephalus* (Zhaoyuan Li *et al.*, 2003). Young leaves are often preferred, despite the fact that they are less abundant than mature leaves, as they are easier to digest (Kirkpatrick, 2007). Some other colobines are better characterised as seed predators, having large proportions of their diets made up of seeds, the classic examples being *Presbytis rubicunda*, whose diet consists of 80% seeds in some seasons (Davies, 1991) and, amongst the African colobines, *Colobus satanas* with seed consumption levels of up to 60% (Harrison, 1986). Seeds provide high energy relative to young or mature leaves and fruit (Dasilva, 1992) and colobine digestive physiology seems well adapted to maximise capture of seed carbohydrates relative to other food sources (Kay and Davies, 1994), showing that seed predation can be a viable strategy for colobines under the right conditions.

In many species, however, this distinction of seed predator versus folivore is not clear cut. Reliance on particular plant organs can be determined by their seasonal or local availability as has been shown for the best studied species. For example, *Nasalis larvatus* show considerable variation in levels of leaf and fruit consumption between studies (Bennett and Sebastian, 1988, Yeager, 1989, Boonratana, 1993, Matsuda *et al.*, 2008). Where some colobine species might reasonably be described as leaf-eaters this does not mean they eat any leaves that are available. They are selective. For example, *Trachypithecus leucocephalus* was found to have a diet of 88% leaves, but over 60% of feeding observations came from only 10 species of plant (Zhaoyuan Li *et al.*, 2003). In general, colobines are “picky eaters”, being quite selective in what species, and what parts of those species, they choose to feed on (Kirkpatrick, 2007).

Data on feeding ecology in the genus *Pygathrix* has to date been based largely on incidental field observations or short-term studies of captive animals. The seminal work of Lippold (1977) on red-shanked doucs (*P. nemaeus*) suggested initially that doucs have quite varied diets, with trees that are fruiting being a determining factor in group movement. Later work (Lippold, 1998) suggested that these doucs were one of the most folivorous of colobines, with a diet consisting of 82% leaf matter. Data from comparative morphology of the gastro-intestinal tract of *P. nemaeus* likewise suggested a largely folivorous diet (Chivers, 1994). This was contradicted somewhat by Pham Nhat (1994), based on his assessment of stomach contents of five red-shanked doucs, which suggested a diet with a considerable fruit component (37%), in addition to a significant leaf element (63%). It should be borne in mind that, unlike most observational field-based feeding ecology studies, stomach content analysis looks at volume as opposed to frequency of feeding records and that standard sampling protocols may underestimate volume of fruit consumption by a factor of five (Chivers and Hladik, 1980).

The somewhat fragmentary nature and methodological differences of these early and important works still left key questions about *Pygathrix* feeding ecology unanswered: how selective are doucs, what are the key species they utilise and how do seasonal changes alter the use of food resources? These questions remained unaddressed until the commencement of the current study in 2002. Since that time several other studies addressing aspects of feeding ecology in doucs have been conducted.

The first was conducted in Cuc Phuong National Park, Vietnam in a four hectare (ha) semi-wild enclosure (Otto, 2005). Although the study was conducted for only 10 days, it showed that a high number of plant species (43) were being utilised by the group of red-shanked doucs. Degree of folivory was lower than had previously been recorded, although the duration of the study meant that considerable sampling error could be expected. While of considerable importance to the management of captive populations of doucs at the Endangered Primate Rescue Center (EPRC), the study's value for understanding wild douc feeding ecology was limited by its short duration.

The most comprehensive feeding ecology research conducted to date is that by Hoang Minh Duc *et al.* (2009), who presented a fascinating description of the feeding ecology of *P. nigripes* in two National Parks in Vietnam, Nui Chua and Phuoc Binh. These parks are radically different from each other in terms of environment and botanical composition (BirdLife International Vietnam Programme and The Forestry Inventory and Planning Institute, 2001), and as such make an ideal study into the degree of dietary flexibility that the species is capable of expressing. While the study was only seven months in duration, it showed a stark difference in approaches between the two douc populations in terms of plant part selectivity, and also documented some seasonal changes in diet, both of which will be explored in more detail in this chapter as they relate to the current study.

While researchers were slow to begin study of the genus *Pygathrix*, the genus is today under ever increasing scrutiny. At the time of writing there are many research projects at many different sites underway which look at the feeding ecology of all taxa of douc (Dinh Thi Phuong Anh *et al.*, 2008, Ha Thang Long *et al.*, 2008, Lippold *et al.*, 2008, O'Brien *et al.*, 2008, Phaivanh Phiapalath and Pongthep Suwanwaree, 2008). It is expected that in the next few years we will finally have a comprehensive understanding of the feeding ecology of the genus and how it varies between species and sites and through seasons. This current chapter is a contribution to this growing understanding and addresses several key questions relating to feeding ecology of the black-shanked douc in Seima Biodiversity Conservation Area (SBCA), Cambodia. I attempt to determine the key components of their diets, how selective they are in relation to plant species exploitation, what are the key resources for them, how diet changes temporally between seasons as well as throughout the day and how all these factors affect issues relating to conservation such as carrying capacity and population protection.

## Methods

In order to determine relative frequencies of exploitation of different plant parts by *P. nigripes*, I used a scan sampling protocol as detailed in Chapter 3. In addition to plant part consumed, the species of tree being utilised was also noted during observations. Approaches to plant species identifications are detailed in Chapter 3. It should be noted that a tree species was only recorded as a food tree if doucs were observed actually eating from it. Information provided by local guides, and fallen fruit and leaves found on the forest floor, were not included in the analysis, as this information can be misleading. Additionally, tree species identification can be problematic in Cambodia due to the lack of a herbarium for comparative assessment and the fact that in many instances there is simply no systematic structure to assign specimens to species in some groups (D. Middleton, in litt.). This is particularly so for the Lauraceae and to a lesser extent the Moraceae and Rubiaceae.

In order to determine how resource use by the doucs tracked resource availability I calculated an availability index for fruits (including seeds), flowers and young leaves for each month for which phenological data were available. The availability index for each plant part was calculated using the following equation:

$$AI = \frac{\sum_i^k ba}{\sum_i^k t} \quad \text{Equation 7.1}$$

Where  $b$  is the basal area of transect tree  $i \dots k$  which has the plant part in question for that month,  $a$  is the abundance score of that plant part on tree  $i$  on a scale of 0-3, determined from monthly phenology walks and  $t_{i \dots k}$  is the basal areas (the cross-sectional area of trees stems at breast height) of all transect trees. This provides an availability index of between 0 and 3.

While many studies use only stem counts to determine resource availability (e.g. Peres, 1994, and see Chapter 4 for this kind of analysis), it has been shown that DBH (diameter at breast height) and associated basal area are good indicators of crown volume and thus abundance (Chapman *et al.*, 1992, Chapman *et al.*, 1994, Phillips, 1995, Heiduck, 2002, Miller and Dietz, 2004) and therefore provide a more accurate estimate of abundance than stem number considered alone. This general approach has been used by several authors (Chapman *et al.*, 1994, Dasilva, 1994, Fashing, 2001). As a simple test of whether these approaches actually measure different variables, I

checked to see how well abundance estimates based on simple stem counts correlated with abundance estimates from Equation 7.1, using Pearson's Correlation Coefficient.

Abundance indices from Equation 7.1 were then tested for correlation with monthly data on consumption of different plant parts (fruit including seed, flowers, and young leaves) taken from behavioural samples using the Spearman Rank Correlation Coefficient, as appropriate for indices. The frequency of a plant part being consumed for a particular month was simply calculated as the number of records for each plant part divided by the total number of feeding observations where a positive identification of plant part was made. A second more restricted statistical test was then performed, including only those plant species that contributed more than 1% of the annual diet, had positive selection ratios, and occurred on transects, similar to Fashing (2001). In this second analysis, fruits and seeds were considered separately to better understand how seed predation at the site tracked seed availability.

Of particular interest for studies on primate feeding ecology is the issue of how selective the species in question is in terms of food items it chooses to eat. I determined what species of plant were selected by doucs at high frequencies relative to their availability within the habitat by calculating a selectivity ratio (*SR*). Calculations followed McKey and Gartlan (1981), except that selectivity ratios were calculated only by tree species, not by plant part within each species, due to low sample sizes for many species. Selectivity ratio was calculated using the following equation:

$$SR_i = \frac{f_i}{b_i} \quad \text{Equation 7.2}$$

Where  $f_i$  is the percentage of feeding records for species  $i$ , and  $b_i$  is the percentage of total basal area for species  $i$  calculated from Transects 1 and 2. Species that are positively selected by the animals have an *SR* of more than 1.0, those that are avoided have a *SR* of between 0 and 1.0, and those that are neutral should have an *SR* of approximately 1.0. In some instances feeding records were made for tree species which were not captured by the transects, which did not allow for the calculation of a selectivity ratio. In these instances the selectivity ratio was merely noted as positive. For additional clarification on selectivity, data on the 15 tree species with the highest summed basal areas calculated from transects were included in the analysis in order to ascertain at what levels these common species in the environment were being utilised.

Daily, seasonal and age and sex class variability in relative frequencies of plant part consumption were assessed using Chi-squared statistical techniques. All statistical tests were performed using SPSS version 12.0.1.

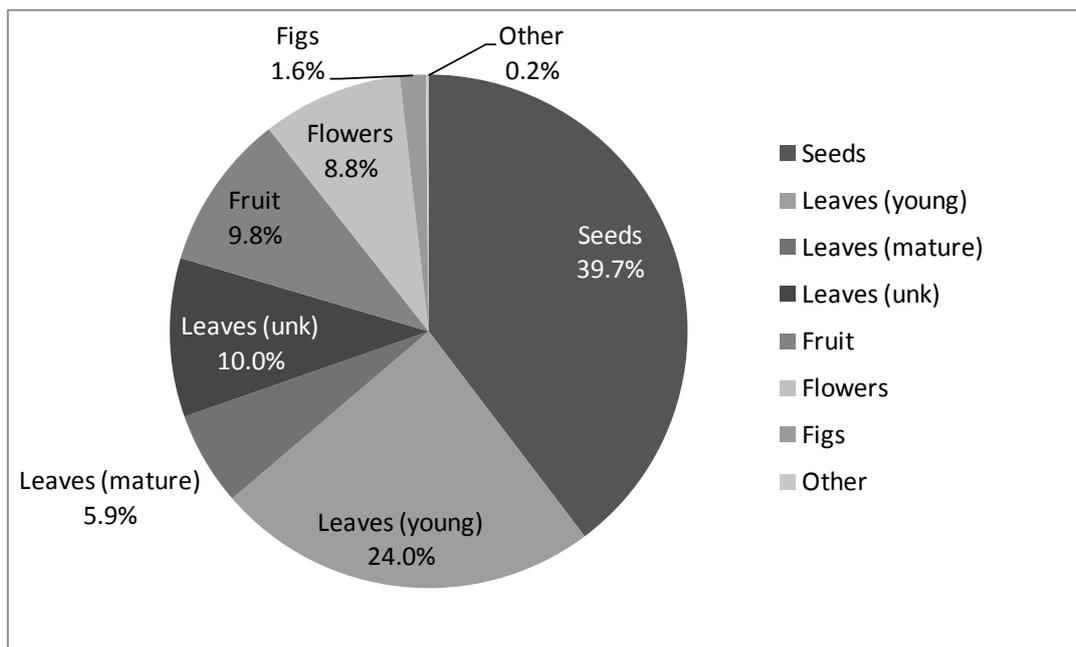
## Results

### *Consumption by plant part*

Feeding behaviour considered the consumption of eight different food types. The relative frequencies of consumption of each food type across the entire study duration, from most frequent to least frequent, with all age and sex classes, excluding infants, grouped together ( $n = 1116$ ), are:

seeds 39.70%,	fruit 9.77%,	figs 1.61%
young leaves 24.01%	flowers 8.78%	other 0.18%.
unknown leaves 10.04%	mature leaves 5.91%	

These percentages are shown in Figure 7-1.



**Figure 7-1** Frequencies for feeding on different food types, age and sex classes grouped, excluding infants ( $n = 1116$ )

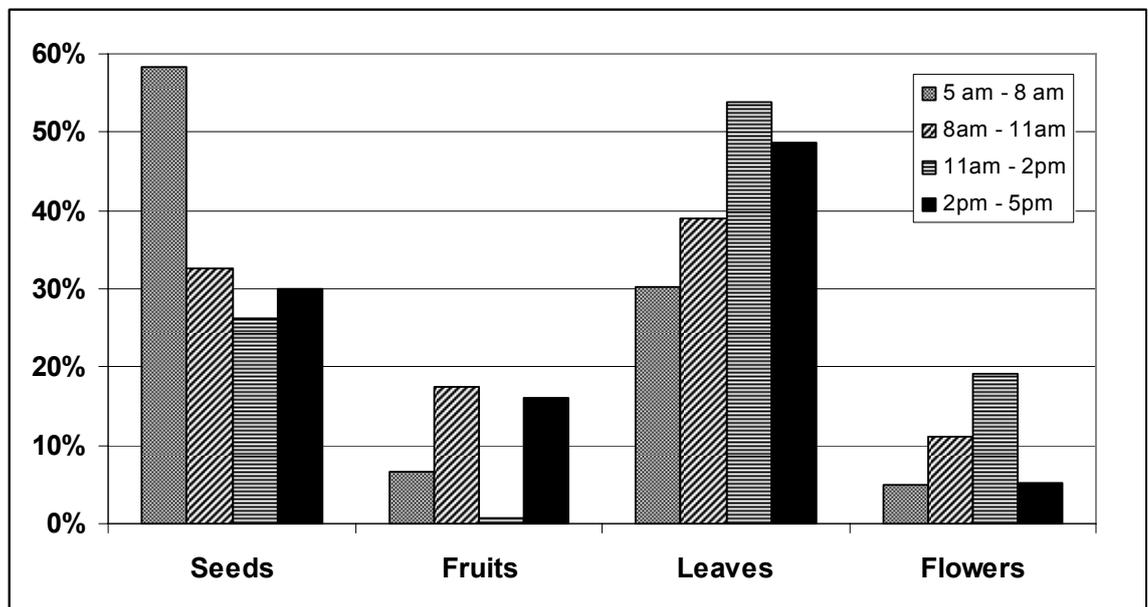
Some studies do not differentiate between some of the feeding subcategories used in this study, so for the sake of comparison grosser divisions are also given here. Using only the categories of fruit, flower, leaves and other (what remains), figures are:

51.08% fruits      8.78% flowers,  
 39.96% leaves      0.18% other.

The only instance of an individual feeding from a food source categorised as “other” occurred when one individual, who was not identified by sex or age category, was seen to be ripping the bark off twigs of a *Dipterocarpus alatus* tree, and consuming it. At no time were doucs seen to drink water from any source, nor even to lick moisture from leaves.

### ***Hourly trends***

Black-shanked doucs at SBCA showed a highly significant association between the time of day and which food items were selected for consumption ( $\chi^2 = 136.21$ ,  $df = 9$ ,  $p < 0.01$ ). Most significantly, seeds were heavily exploited at the expense of all other food types in the early morning (see Table 7-1 and Figure 7-2) with levels considerably higher than would be expected from the general patterns of Figure 7-1. This preference changed during the rest period over midday with fruits and seeds then under-represented and leaves and flowers over-represented. There was no clear pattern of targeted exploitation in the evening before the doucs stopped activities for the day.



**Figure 7-2** Percentage of food items eaten at different times of the day ( $n = 1114$ ).

Time	Seeds	Fruit	Leaves	Flowers
5 am-8 am	58.27	6.50	30.35	4.88
8 am-11 am	32.61	17.39	38.86	11.14
11 am-2 pm	26.24	0.71	53.90	19.15
2 pm-5 pm	30.08	16.10	48.73	5.08

**Table 7-1** Percentage of food items eaten at different times of the day ( $n = 1114$ ).

### *Age and sexual variation*

As noted in Chapter 5, variation in feeding frequency was detected, with males feeding less frequently than expected and immatures more ( $\chi^2 = 14.916$ ,  $df = 2$ ,  $p = < 0.01$ ). The data show considerable age and sex variation in consumption of different food types ( $\chi^2 = 58.511$ ,  $df = 10$ ,  $p = < 0.01$ ) (Figure 7-3). Male diets were dominated by seeds, with a frequency of almost 60%. Female and immature consumption of seeds was still high, but considerably lower than males', with frequencies of 43.8% and 34.8% respectively. Conversely, male consumption of leaves was relatively low, with levels of 22.1% overall, compared to females who consumed leaves at almost twice the frequency with 40.9%, and immatures at 36.8%. Other food items played a lesser role in the diet of all animals. For both fruits and flowers females had the lowest consumption frequencies followed by males and immatures. Figs were eaten infrequently, but with high intensity.

Sub-category	Female	$n$	Male	$n$	Immature	$n$
Seeds	43.8%	154	59.3%	166	34.8%	71
Leaves (imm)	25.9%	91	9.0%	25	17.7%	36
Leaves (unk)	9.9%	35	8.2%	23	13.2%	27
Fruit	8.8%	31	11.0%	31	14.2%	29
Flowers	4.5%	16	7.5%	21	12.7%	26
Leaves (mat)	5.1%	18	5.0%	14	5.9%	12
Figs	2.0%	7	0.0%	0	1.5%	3

**Table 7-2** Frequencies for feeding on different food types, by age and sex class ( $n_{\text{female}} = 352$ ,  $n_{\text{male}} = 280$ ,  $n_{\text{immature}} = 204$ ).

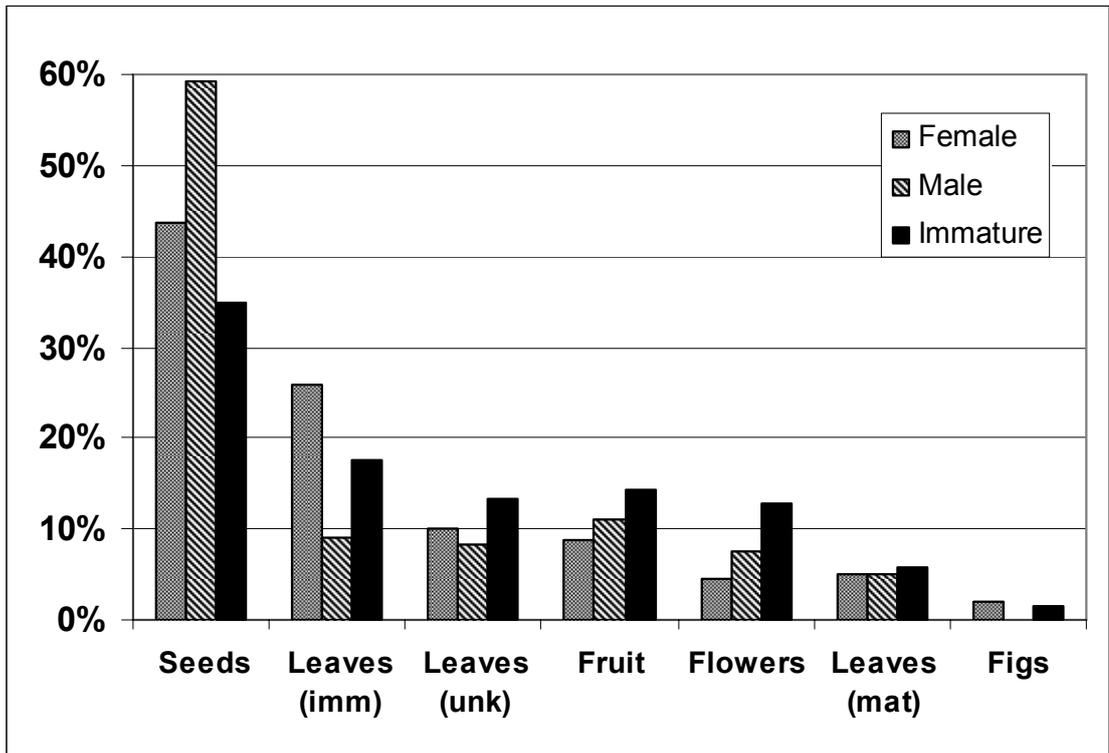


Figure 7-3 Frequencies for feeding on different food types, by age and sex class ( $n_{\text{female}} = 352$ ,  $n_{\text{male}} = 280$ ,  $n_{\text{immature}} = 204$ ).

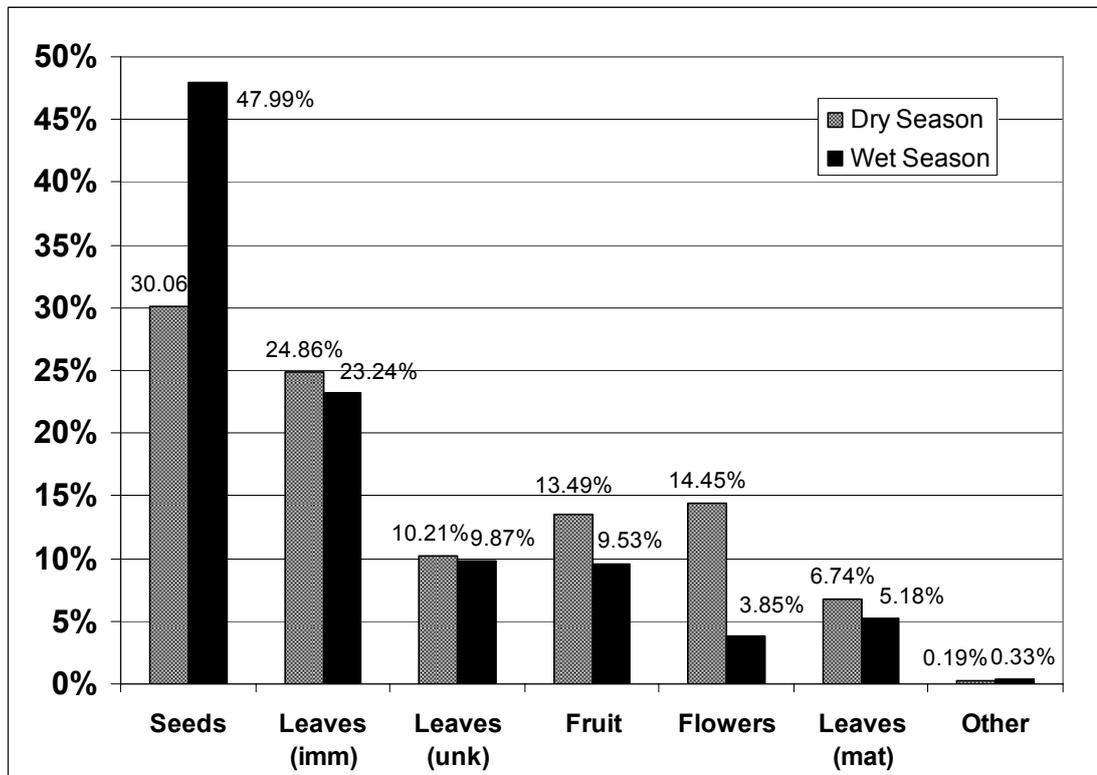


Figure 7-4 Frequencies for feeding on different food types, by season ( $n_{\text{dry}}=519$ ,  $n_{\text{wet}}=598$ ).

## ***Seasonal variation***

Diet was significantly different in the dry season (November – April) compared to the wet (May – October) ( $\chi^2 = 63.045$ ,  $df = 4$ ,  $p < 0.01$ ) (Figure 7-4). Most notably, feeding on seeds was considerably under-represented in the dry season (30%) and over-represented in the wet season (48%). This discrepancy was reduced, however, when fruits and seeds were analysed as one food type (data not shown). Conversely, consumption frequencies of flowers were considerably higher in the dry season (14.5%) than in the wet season (3.8%). Consumption of leaves in all categories was similar between seasons, with total frequencies of 38.3% in the wet and 41.8% in the dry. There were no significant differences in consumption of immature or mature leaves by season.

## ***Consumption versus availability***

Indices were calculated to determine whether resource use was tracking resource availability. Resource availability of fruit (including seeds), flowers and young leaves was used to calculate a monthly availability index (see Equation 7.1, Methods section). This availability index was then tested for a correlation with abundance estimates derived from the percentage of stems with a plant part confirmed as present for each month, to determine whether these different methods return radically different abundance levels. It was found that for all plant parts on both transects, there was a highly significant correlation between methods (Table 7-3). While both methods appear to track abundance, the availability index, which uses basal area and abundance estimates from phenology data was used for all subsequent analysis based on its assumed higher accuracy.

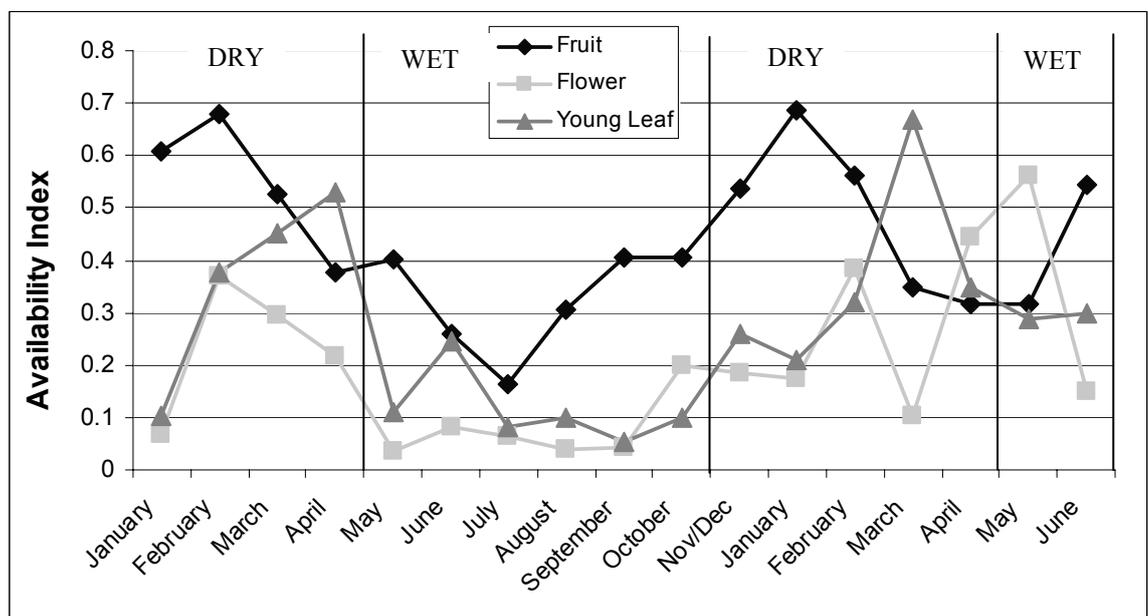
	Percentage of Stems with Plant Part Present		
Availability Index	Fruit	Flower	Young Leaf
Transect 1	0.722**	0.712**	0.719**
Transect 2	0.679**	0.819**	0.920**

**Table 7-3** The correlations between calculated availability indices using Equation 7.1 and simple stem counts of phenology trees with a plant part confirmed present (Pearson correlation values and probabilities are given).

\*\*  $p < 0.01$

I also tested whether Transects 1 and 2 were correlated in terms of the calculated relative abundances by month (see Chapter 4 for descriptions of transects). Abundance of fruits ( $r_s = 0.485$ ,  $n = 17$ ,  $p = 0.048$ ) and flowers ( $r_s = 0.569$ ,  $n = 17$ ,  $p = 0.017$ ) on the

two transects were strongly correlated, this was less so for young leaf abundance ( $r_s = 0.407$ ,  $n = 17$ ,  $p = 0.105$ ). Transect 2 showed higher spikes in young leaf abundance index scores during the end of the dry/start of the wet season transition. Transects data were pooled to create a single availability index for comparison with feeding data. Calculated availability indices for fruit (including seeds), flowers and young leaves across the entire study based on all transect trees are shown in Figure 7-5. Fruits and seeds were not differentiated in this analysis as not all trees were exploited by the doucs and not all trees were identified, and therefore a classification other than broadly “fruit” was not possible.



**Figure 7-5** Availability indices of fruits (including seeds), flowers and young leaves by month based on all trees in Transects 1 and 2 for years 2003 and 2004.

Only from seven consecutive months, December 2003 to June 2004, were data available for a matching analysis of resource availability and douc consumption of plant parts. This was due to insufficient numbers of feeding observations in some early months of the study and lack of phenology data in the last month of the study. Two analyses were conducted using all transect trees. Firstly I looked at the availability of fruit (including seeds for the reasons given above), flowers and young leaves and compared availability to consumption. Consumption of these plant parts, did not correlate with their calculated availability indices from all transect trees ( $n = 436$ ) during this period (see Table 7-4 for  $r_s$  values and significance levels).

Secondly, I looked at availability and consumption correlations based only on those transect tree species that were exploited by doucs during the study, based only on tree species which constituted >1% of diet, had positive selection ratios, and were present on transects (see Table 7-6). For these nine species ( $n = 35$ ), availability indices were calculated for only those plant parts that doucs had been seen to consume (see Table 7-5). Results showed no correlation between consumption and availability indices for fruits and seeds combined, fruit and seed assessed independently, or young leaves, but flower availability and consumption were significantly positively correlated (see Table 7-4). This links well with the observation that flower consumption peaks in the dry season (Figure 7-4), when flower availability is highest (Figure 7-5).

	<i>n</i>	Plant Part				
		Fruit & Seeds	Fruit	Seeds	Flower	Young Leaf
Available vs. consumed: all species	436	0.091 (ns)	NA	NA	-0.109 (ns)	-0.429 (ns)
Available vs. consumed: important species	35	-0.607 (ns)	-0.027 (ns)	0.111 (ns)	0.787*	-0.036 (ns)

**Table 7-4** Spearman correlation coefficient ( $r_s$ ) values for comparison of plant part consumption versus plant part availability across seven months. Values for availability based on all trees from transects (all species) and based on species constituting >1% of diet, present on transects and with positive selection ratios (important species).  $n$  = number of transect trees included in each calculation of availability.  
\*  $p < 0.05$

I also tested for correlation between fruit (seed and fruit) availability and young leaf consumption, hypothesising that there would be a negative correlation between these variables; but there was no significant correlation based on abundance indices calculated using all transect trees ( $r_s = -0.309$ ,  $n = 7$ ,  $p = 0.50$ ) or only important species ( $r_s = -0.179$ ,  $n = 7$ ,  $p = 0.70$ ), and no correlation when using only preferred seed availability and young leaf consumption ( $r_s = 0.222$ ,  $n = 7$ ,  $p = 0.63$ ).

### ***Dietary diversity and selectivity***

In total, doucs were recorded feeding from 190 trees during the study. Of these, 139 or 73% were identified to the level of family, 137 or 72% to the level of genus and 96 or 51% to the level of species (see Table 7-5). Identified trees came from 21 families and 32 genera. From these species the recorded diet consisted of 54 food items (see Table 7-5). However, there were large numbers of feeding records taken from unidentified trees

and lianas. In total 51 tagged trees, which consisted of up to 46 species, were unidentifiable either because samples could not be collected, or were sterile, or were fertile but still could not be identified. In total, only 32% of identified transect tree species were exploited by doucs during this study. This number is reduced to 19% if one includes unidentified trees species from transects and assumes each is the only representative of its species on the transects. Conversely, 66% of identified feeding trees occurred on transects, although again due to the large number of unidentified transect trees this number may be higher.

Selectivity ratios (*SR*) were calculated for the 15 plant species with the most feeding records made from behavioural observations (see Table 7-6). Only the top 15 are included in analysis as sample sizes beyond this point were too small for any meaningful analysis. As botanical transects did not capture 100% of tree species occurring at the site, some species were utilised as food items but no information on their relative basal area was available, meaning that no selectivity ratio could be calculated. Where this was the case, these species have been marked with a “+” to denote that they have positive selection ratios of an unknown quantity. Conversely, some species that were common on transects were never observed to be fed on; these species are denoted as “-”, showing merely that they have a negative selection ratio which can not be quantified.

It can be seen from Table 7-6 that the most heavily positively selected species are *Peltophorum cf. dasyrrhachis*, *Syzygium sp.*, *Irvingia malayana*, *Azelia xylocarpa* and *Sindora siamensis*. Three of the top five are legumes (atmospheric-nitrogen-fixing plants by virtue of the bacterial nodules on their roots) and it appears that these are heavily selected by the black-shanked doucs at the site. The three most underselected species are *Xylia xylocarpa*, *Largerstroemia cf. calyculata*, and *Microcos tormentosa*. These three species were very common in the study area, ranked respectively first, second and fifth, but were rarely utilised as food by the doucs.

#	Family	Species	No.	Y leaf	m leaf	flow	seed	fruit
1	Anacardiaceae	<i>Dracontomelon</i> sp.	8				+	
2	Annonaceae	<i>Melodorum</i> sp.	1	+				+
3	Aquifoliaceae	<i>Ilex umbellata</i>	1					+
4	Bombacaceae	<i>Bombax anceps</i>	1			+		
5	Combretaceae	<i>Anogeissus acuminata</i>	8	+			+	
6	Combretaceae	<i>Terminalia</i> sp.	7				+	
7	Datisceae	<i>Tetrameles nudiflora</i>	1	+	+			
8	Dilleniaceae	<i>Dillenia</i> sp.	1					+
9	Dipterocarpaceae	<i>Dipterocarpus alatus</i>	3	+				
10	Dipterocarpaceae	<i>Hopea odorata</i>	2	+				
11	Fabaceae	<i>Acacia concinna</i>	2				+	
12	Fabaceae	<i>Azelia xylocarpa</i>	21	+		+	+	
13	Fabaceae	<i>Albizia myriophylla</i>	1				+	+
14	Fabaceae	<i>Bauhinia</i> sp	2			+		
15	Fabaceae	sp.	2				+	+
16	Fabaceae	<i>Millettia</i> sp.	9	+	+	+	+	
17	Fabaceae	<i>Peltophorum cf. dasyrrhachis</i>	5				+	
18	Fabaceae	<i>Sindora siamensis</i>	14	+			+	
19	Fabaceae	<i>Xylia xylocarpa</i>	4	+				
20	Hypericaceae	<i>Cratoxylum</i> sp.	1	+				
21	Irvingiaceae	<i>Irvingia malyana</i>	16	+	+	+		+
22	Labiatae	<i>Vitex</i> sp2.	1					+
23	Lythraceae	<i>Lagerstroemia cf. calyculata</i>	5		+	+		
24	Lythraceae	<i>Lagerstroemia</i> sp.	3	+				
25	Meliaceae	<i>cf. Agalia</i>	2			+		
26	Meliaceae	<i>Dysoxylum</i> sp.	1				+	+
27	Meliaceae	<i>Heynea velutina</i>	4		+		+	+
28	Myrtaceae	<i>Syzygium</i> sp.	1				+	
29	Moraceae	<i>Ficus racemosa</i>	1					+

30	Moraceae	<i>Ficus</i> sp.	1					+
31	Rhamnaceae	<i>Ziziphus cambodiana</i>	5	+				+
32	Rubiaceae	<i>Haldina cordifolia</i>	1		+			
33	Sapindaceae	<i>Nephelium hypoleucum</i>	1				+	
34	Staphylaeaceae	<i>Turpinia</i> sp.	1					+
35	Sterculiaceae	<i>Pterocymbium</i> sp.	2			+		

**Table 7-5** Positively identified plant taxa that *Pygathrix nigripes* was observed feeding from, the number of individuals for each species and the plant part(s) that was consumed.

Rank SR	Rank Basal Area	Species	Stems	% of Feeding Records	% of Basal Area	Selection Ratio
1	39	<i>Peltophorum cf. dasyrrhachis</i>	1	10.8%	0.4%	25.08
2	14	<i>Syzygium</i> sp.	4	4.1%	0.6%	6.64
3	31	<i>Irvingia malayana</i>	6	11.7%	1.6%	6.46
4	10	<i>Azelia xylocarpa</i>	2	11.0%	1.9%	5.76
5	21	<i>Sindora siamensis</i>	6	3.0%	1.0%	2.86
6	17	<i>Lagerstroemia</i> sp	2	3.6%	1.4%	2.54
7	7	<i>Terminalia</i> sp.	8	3.2%	3.3%	0.98
8	3	<i>Anogeissus acuminata</i>	9	6.1%	7.1%	0.85
9	4	<i>Millettia</i> sp.	4	4.1%	5.4%	0.76
10	-	<i>Hopea odorata</i>	0	3.6%	0.0%	+
11	-	<i>Dysoxylum</i> sp.	0	3.0%	0.0%	+
12	-	<i>cf. Agalia</i> sp.	0	2.8%	0.0%	+
13	-	<i>Ficus</i> sp.	0	1.5%	0.0%	+
14	2	<i>Xylia xylocarpa</i>	26	0.9%	8.2%	0.11*
15	1	<i>Lagerstroemia cf. calyculata</i>	49	1.7%	21.5%	0.08*
-	5	<i>Microcos tomentosa</i>	35	0.0%	5.1%	-
-	6	<i>Vitex</i> sp3.	19	0.0%	4.0%	-
-	8	<i>Dolichandrone</i> sp.	1	0.0%	2.8%	-
-	9	<i>Pterocarpus macrocarpus</i>	2	0.0%	2.0%	-
-	11	<i>Dipterocarpus cf. costatus</i>	9	0.0%	1.8%	-
-	12	<i>Careya arborea</i>	6	0.0%	1.7%	-
-	13	<i>Vitex</i> sp2.	12	0.2%	1.7%	0.15*
-	15	<i>Bombax anceps</i>	3	0.0%	1.5%	-

**Table 7-6** Selection ratios for the 15 plant species with the greatest number of feeding records ( $n = 899$ ).

\* denotes a negative selection ratio.

+ denotes a positive selection ratio with no associated figure as the species did not occur on transects.

- denotes a negative selection ratio with no associated figure as the species did not occur in feeding records.

## Discussion

### *What is the Pygathrix nigripes feeding niche?*

Feeding data presented in this chapter show that *P. nigripes* in SBCA has a diet which is co-dominated by leaves and, more significantly, seeds. Flowers complemented the doucs' basic diet significantly, especially in the dry season, and considerable amounts of fruits are also consumed. Figs are a preferred resource when available, although fig tree density is low at the site meaning that this resource was seldom available. The paradigm of the Colobinae as "leaf eating monkeys" has had to be considerably modified, and it is worthy of note that black-shanked doucs appear to continue the trend of possessing dietary diversity and reliance on a range of resources as evidenced by other Colobinae. A summary of research on douc feeding ecology is presented in Table 7-7. The general progressive history of *Pygathrix* feeding ecology is described in detail below before final conclusions based on the current research are discussed.

The work of Pham Nhat (1994) in Vietnam represents the first information on diet for the genus *Pythagrix*, derived from a mixture of analysis of stomach contents and "field records"; it is not clear how or where such records were obtained, nor which record pertains to which data source presented. He presented some 50 plant species from 20 families, of which the only overlap with plant genera presented in the current study is the highly overselected *Peltophorum*, and *Ficus* and *Dillenia*. Lack of overlap is probably an indication of the very different habitats of the present study site and the areas within Vietnam where *P. nemaesus* occurs. Assessment of relative exploitation of leaf versus fruit is given as 63% and 37%, which is superficially similar to figures presented in this study; the percentage of seed exploitation is not presented.

Further important preliminary information on douc feeding ecology was given by Lippold (1998) based on timed observations of feeding behaviour in a number of protected areas in Vietnam. In contrast to the current study, her data suggest doucs are highly folivorous with 82% of diet comprised of leaf matter and 14% made up of fruits and seeds. These high levels of folivory may represent accurate estimates or may be an artifact of small sample size; it is difficult to make a thorough comparison with the current study because of different methodological approaches (timed observations versus frequencies), because details of the data are not presented, and because plant species were not identified. Regardless, this work provided the basis of our understanding on douc feeding ecology for a decade.

Otto (2005) provided some additional data on red-shanked douc feeding ecology from her 10-day study on semi-free ranging doucs inhabiting a 4 ha fenced area containing primary forest on limestone karst in Cuc Phuong National Park, Vietnam. Her results suggest a lower level of folivory than those of Lippold (1998), with similarly low levels of fruit consumption but very high levels of flower consumption (25%), which exceed most figures for Asian colobines (see Table 7-7). This high level of consumption of flowers most likely represents sampling error, given that a highly preferred species of flower, *Garuga pinnata*, was flowering during the study period, resulting in the highest number of visits for any species (along with the fruiting *Loeseneriella pauciflora*). Her results suggest that while folivory may be the dominant strategy, at least in this environment, when other options are available doucs will gorge themselves on other food items.

Despite the fact that Otto's study period was only 10 days, 43 species from 24 families of food plant were recorded; legumes were the most commonly consumed food type, with six species comprising 14% of all species records (Otto, 2005). This large diversity of diet recorded within such a short period of time on these habituated red-shanked doucs is in stark contrast to levels of dietary diversity presented in the current study for *P. nigripes*. It should be noted, however, that *P. nemaesus* does not occur naturally in Cuc Phuong National Park (Nadler *et al.*, 2003) and the species is not a limestone (forest) specialist, a habitat which has very high species diversity (Clements *et al.*, 2006) and generally low levels of fruit production, possibly requiring consumption of a diverse diet.

The most relevant source for comparison with the present study is the work of Hoang Minh Duc and colleagues (Hoang Minh Duc and Baxter, 2006, Hoang Minh Duc *et al.*, 2009) in Nui Chua and Phuoc Binh National Parks, Vietnam. Levels of plant part consumption at both of these sites were remarkably similar, given the very different species composition within the parks, altitudinal variation and levels of annual rainfall (BirdLife International Vietnam Programme and The Forestry Inventory and Planning Institute, 2001). At both sites leaves were the dominant food item consumed, with frequencies of 54.4% and 54.7% respectively. Fruits (including seeds) comprised 31.6% and 27.4% at the two sites, with seed consumption comprising 9.6% of total observations, and flowers 14.6%, averaged across the two sites. The sites show considerably higher levels of leaf consumption and considerably lower levels of seed

consumption relative to the present study; the period of study was only seven months so some sampling error might be expected.

Variation in diets between the 2009 Vietnam study (Hoang Minh Duc, 2007) and the current study in SBCA, Cambodia, can be explained as follows. First, both of these protected areas in Vietnam comprise habitats very different from SBCA. Nui Chua is highly disturbed, receives less than 650 mm of rain per year (about 1/5<sup>th</sup> of SBCA), contains large areas of thorny forest with high plant diversity (1265 species recorded) (Hoang Minh Duc *et al.*, 2009), and has an altitudinal range of over 1000 m (BirdLife International Vietnam Programme and The Forestry Inventory and Planning Institute, 2001). Phuoc Binh also has a large altitudinal gradient with a high point of almost 2000 m ASL (compared to about 200 m ASL in SBCA) and has an annual rainfall of >2000 mm but with lower plant species diversity with 513 recorded species (Hoang Minh Duc *et al.*, 2009). The sites are also considerably different from each other in botanical species composition (BirdLife International Vietnam Programme and The Forestry Inventory and Planning Institute, 2001).

Differences may therefore simply be a result of different plant species compositions and phenological cycles at each site, although one would have expected larger differences between Nui Chua and Phuoc Binh NPs given their very different characteristics. No phenological data on plant part availability were collected during this work however (Hoang Minh Duc *et al.*, 2009), and so whether higher leaf consumption at these sites relative to SBCA represents lower availability of apparently preferred foods such as seeds of the Legumes, or an alternative foraging strategy, is unknown.

Alternatively, or additionally, the study in Nui Chua and Phuoc Binh NPs was conducted between February and August 2005, and as such it is difficult to assess whether these percentages of food type exploitation represent seasonal or annual averages. It may be that the frequencies are actually more representative of wet season diets (especially in Phuoc Binh NP) when alternative plant parts to leaves may (or may not) be readily available, positively skewing leaf consumption frequencies relative to the current study.

Ultimately however there is considerable diversity in results obtained thus far for *Pygathrix* feeding ecology. This probably reflects natural variation brought about by different habitat types and floral species compositions at different sites, in some cases

radically different. Furthermore, variation is likely to occur even within habitat types and sites due to macro environmental differences; group size and composition; individual preference; and any number of other variables. This variability in feeding selectivity, between groups within sites (Huang *et al.*, 2000, Zhaoyuan Li *et al.*, 2003) and even within groups across years (Chapman *et al.*, 2002), has been documented for other colobines. In addition to this intrinsic variability, considerable variation in study design (stomach contents analysis, semi-free ranging animals, small sample sizes etc) probably plays a significant role.

For the benefit of completeness it is worth making comparisons further afield than the genus *Pygathrix*, into species that also apparently form part of the same clade, the odd-nosed monkeys (Roos *et al.*, 2008b). Genetic analysis suggests that genus *Pygathrix* is the sister group to a *Nasalis/Simias* clade (Roos *et al.*, 2008b), while divergence from the genus *Rhinopithecus* occurred more distantly, perhaps seven million years ago (see Chapter 1 for a full discussion). Unfortunately no comparative feeding ecology data are available for *Simias concolor*, but several studies have looked at the feeding ecology of *Nasalis larvatus* (Bennett and Sebastian, 1988, Yeager, 1989, Boonratana, 1993, Matsuda *et al.*, 2008), some details of which are presented in Table 7-7. It can be seen that overall levels of leaf and fruit/seed consumption are similar between the taxa, while seed consumption is considerably higher in *P. nigripes* than *N. larvatus*, and fruit consumption lower; facts which match well with comparative gut anatomy for these species (Chivers, 1994).

The Vietnamese *Rhinopithecus avunculus* probably represents the only species from its genus that can be sensibly compared with *Pygathrix* given that the Chinese representatives of the genus live in high altitude, highly seasonal coniferous areas with highly specific diets (Bleisch and Xie Jiahua, 1998, Yiming Li, 2001, Yang and Zhao, 2001, Xiang *et al.*, 2007). Interestingly, the most recent and comprehensive feeding ecology studies from *R. avunculus* show an almost identical degree of leaf consumption but considerably higher levels of fruit/seed consumption (Dong Thanh Hai, 2008) than found in this study for *P. nigripes*, although the majority of these records come from consumption of fruit (47%) rather than seeds (15%), which suggests that the species is taking a different adaptive approach.

Amongst the other Asian colobine genera *Presbytis*, *Trachypithecus* and *Semnopithecus* (Table 7-7) variation is considerable. Most *Presbytis* and *Trachypithecus* species have

considerably higher consumption of leaf material and lower frequencies of fruit, especially seed consumption (when this has been measured). One exception apparently confirmed from two studies is *Presbytis rubicunda* (Supriatna *et al.*, 1986, Davies, 1991). Supriatna *et al.* (1986) found levels of leaf and fruit consumption similar to *P. nigripes*, although no subcategories were used so it is unclear what fraction of fruit consumption was composed of seeds. Davies' (1991) study was more comprehensive and concluded that *Presbytis rubicunda* is a seed predator, with seeds consumed in large quantities during the fruiting season and preferred over pulpy fruit, which were consumed when large seeded fruits were less available. The seeds of legumes constituted an important part of the diet, comprising 28% of fruit consumption (Davies, 1991).

Ultimately, based on data presented within this chapter, it seems that *P. nigripes* in SBCA is also best characterised as a seed predator, with preferential selection and processing of seeds when available. Larger seeds are not likely to be dispersed, as they are unlikely to survive mastication and gut passage. The fate of smaller seeds is unknown, although faecal material generally showed no whole seeds. In one instance large numbers of fig seeds were found in faeces, but their viability was not tested. Leaf consumption comprised a similar proportion of feeding events to seeds, but they appear to be less preferred than seeds when the latter are available. Seeds, relative to leaves, are high in fats and energy but low in nitrogen and ash; but they are also low in phenols, tannins and other digestion inhibitors (McKey and Gartlan, 1981, Dasilva, 1994). Fruits and, seasonally, flowers subsidised the diet. While figs were clearly a preferred food item, as they were in Hoang Minh Duc's (2007) study, frequency of consumption was low, probably because of low availability in this region (see Chapter 4). Insects were not seen to be actively predated, although doubtless there is some incidental consumption when feeding on plant parts. Water was never seen to be consumed during the study, not even licked off leaves as with observations of wild *P. nemeus* (Lippold, 1977).

Black-shanked doucs at the site also show a marked dietary preference for the Legumes, with considerable seed exploitation and supplementary leaf exploitation of several species. The Legumes, with their atmospheric-nitrogen-fixing ability, appear to be a common target of leaf eating monkeys, and the black-shanked doucs of SBCA seem to be no exception. It has been proposed that legume seed predation is a tactic which may be linked to poor acidic soils (Maisels *et al.*, 1994). In these conditions, legumes may

thrive relative to other plant families because they do not depend solely on soil nitrogen for their growth, and provide a large source of nutrient rich seeds which colobines can then exploit (Maisels *et al.*, 1994). Soil composition in SBCA was not tested, and so no generalisations can be made, but soil types apparently vary locally within the site (Zimmermann and Clements, 2002) and as such so might legume abundance and possibly douc carrying capacity.

The doucs at the site show quite low dietary diversity. Only 35 species of feeding tree were identified, although the real number is certainly considerably larger given that many species that were consumed, especially lianes, were never positively identified. This is similar to the number of species (39) reportedly eaten by black-shanked doucs in Phuoc Binh NP, but considerably lower than for Nui Chua NP (135 species) (Hoang Minh Duc *et al.*, 2009). The reason for this discrepancy is discussed in more detail below; it almost certainly relates to the considerably higher plant diversity in Nui Chua NP and the probable low quality of feeding resources there.

With a few notable exceptions there was little overlap in terms of species consumed between the current study and that of Hoang Minh Duc (2007) in Nui Chua and Phuoc Binh NPs. One of these exceptions was the high level of consumption of *Sindora siamensis*, being the species with the most feeding records in his study (6.7%), with these predominantly coming from seeds. This species ranked five in selectivity indices in SBCA with 3% of all feeding records. *Irvingia malayana* was also heavily exploited in both studies with 6.25% of feeding records from Nui Chua and Phuoc Binh NPs, and 6.46% in the current study. Interestingly, no fruit was seen to be consumed in Hoang Minh Duc's (2007) study despite the fact that, based on phenological cycles of the species in SBCA, it would be expected to be fruiting during his study period. Similarly, a *Peltophorum* species from his study was quite heavily exploited, but only for leaves, not seeds unlike in SBCA. The heavy use of *Sindora siamensis* and *Irvingia malayana* in both studies suggest these species may be important across the range of black-shanked doucs.

The black-shanked doucs in SBCA also showed high levels of selectivity, suggesting that here at least they are fussy eaters. The top five most utilised species constituted 43.7% of feeding records and the top 15 constituted 71.1%. Looking at other odd-nosed colobines, it appears that *Rhinopithecus avunculus* is also a highly selective feeder (Dong Thanh Hai, 2008) while *Nasalis larvatus* is not (Matsuda *et al.*, 2008), while

information from *Simias* is lacking and other species of *Rhinopithecus* are not directly comparable.

The niche of *P. nigripes* in SBCA contrasts with other sympatric primates. Gibbons' (*Nomascus gabriellae*) focus is on pulpy fruits, and while consumption of seeds may occur, these generally pass through the gut unharmed and even, at least in one gibbon species, play an important role in seed dispersal and forest health (McConkey, 2000, McConkey and Chivers, 2007). The three species of macaque at the site (*Macaca fascicularis*, *M. leonina* and *M. arctoides*) are all apparently generalists (although no data are available on their ecology in Cambodia) feeding on a wide array of plant and animal materials and avoiding competition through habitat and canopy segregation. While some competition may occur over soft highly preferred fruits such as figs, generally dietary overlap is small, macaques' use of leaf material and seeds being minimal. Silvered langurs, currently recognized as *Trachypithecus margarita* (Roos *et al.*, 2008a), may have considerable dietary overlap with *P. nigripes*, but seem to be generally restricted to riverine forest in more deciduous areas at the site and as such competition may be reduced through different habitat preferences. Niche separation from *Nycticebus* spp. is obvious, given the latter's nocturnal habitats and reliance on exudates and nectar (Streicher, 2004). This niche differentiation and focus on relatively common resources, which other primates are unable to access, allows sympatry of multiple primate species at the site, and also allows for the high relative densities of *P. nigripes* in these forests (Pollard *et al.*, 2007).



**Table 7-7** Percentage contribution of different plant parts to diet in several Asian colobine species.

## ***Do diets of *Pygathrix nigripes* track resource abundance and energy requirements?***

Resources that primates rely on, such as fruit, flowers and leaves, are expected to show fluctuation throughout the year in their availability (Peres, 1994). This was clearly the case at the study site, based on abundance indices generated from phenology data. Availability of resources was calculated using an index which takes into account both the number of trees with a particular plant part in any given month, the basal area of those trees, and the relative abundance of the plant part at the time of measurement. Other studies (e.g. Peres, 1994, Fashing, 2001, McConkey *et al.*, 2002, McConkey *et al.*, 2003) have used simpler indices of abundance which do not take into account basal area or DBH, but merely use the percentage of trees with a particular plant part. It has been shown, however, that DBH, and by extension basal area, correlates well with crown volume and abundance (Chapman *et al.*, 1992, Chapman *et al.*, 1994, Phillips, 1995, Heiduck, 2002, Miller and Dietz, 2004). This is simply because larger trees generally produce a greater abundance of resources, whether they be fruits, flowers or young leaves, than a smaller tree of the same species (Miller and Dietz, 2004).

The index of abundance, calculated using basal area shown in Equation 7.1, was significantly correlated with the simpler measure of number of stems with a plant part, suggesting that the two methods assess the variable of abundance in similar ways. This was also found to be the case by other authors (Chapman *et al.*, 1994, Fashing, 2001), as Chapman *et al.* (1994) note, there is no way of determining actual abundance levels, and as such we are left not knowing which may be the more accurate approach. The abundance index was used here, based on its assumed higher accuracy (Chapman *et al.*, 1992, Chapman *et al.*, 1994, Phillips, 1995, Miller and Dietz, 2004).

Results of this analysis showed no correlation between the consumption of specific plant parts on a monthly basis, and the availability of those specific plant parts based on abundance indices calculated from all transect trees. Such an approach has methodological shortcomings, however, for while such indices may represent the general availability of these resources in the environment, it does not take into account the selectivity in resource use that the foraging species in question applies. In other words, site wide abundance is not interchangeable with the abundances of the subset of resources utilised by the doucs, as they utilise only a proportion of the available tree species (Hemingway and Overdorff, 1999).

In order to counter this, I conducted an additional analysis using only abundance of known species utilised. This approach attempts to replicate the selected tree method (Hemingway and Overdorff, 1999) *post hoc*. Sample sizes of some species are of course small, with only 35 trees to draw from and some utilised species did not even occur on transects, including four of the top fifteen most positively selected plant species (see Table 7-6). Results are probably further obfuscated by the fact that this study probably did not capture all feeding tree species on which doucs at the site rely.

Ability to detect trends in consumption and abundance is therefore very limited, and only a correlation between flower abundance and utilisation was detected. This relates to the highly seasonal levels of availability of flowers; with a clear peak during the end of the dry season and a virtual absence from phenology transect trees during the bulk of the wet season as shown in Figure 7-5. Doucs clearly take advantage of high flower abundance during this period and selectively feed on them at higher levels than at times of lower abundance (Figure 7-4). This is consistent with Hoang Minh Duc *et al.*'s study in Nui Chua and Phuoc Binh NPs, where black-shanked doucs fed on flowers considerably more in the dry season than the wet season. No phenological data were available for their study, however, so it is unclear whether this trend is influenced by higher flower availability in the dry season as apparently is the case in the current study.

While availability and consumption indices did not show that doucs were tracking resource availability of fruits, seeds and young leaves, data from observed versus expected frequencies showed that at least consumption of seeds was seasonal, with higher levels than expected in the wet season and lower levels than expected in the dry season (Figure 7-4). Data were not sufficient to ascertain whether this tracks availability in these seasons, but seeds are clearly a preferred resource and heavily exploited. Hoang Minh Duc *et al.* (2009) also noted that levels of fruit consumption (seeds plus fruit) were higher for doucs in the wet than the dry season in Nui Chua and Phuoc Binh NPs, but as seeds and fruit were not differentiated it is unclear whether the same pattern is happening at these sites. Fruit, when considered separately to seeds, showed no strong seasonal trends in consumption or availability in the current study.

For young leaves however, temporal trends in availability were clear, with a site-wide new leaf flush just prior to the onset of the rainy season (see chapter 4 and Figure 7-5). Despite this noticeable increase in the availability of this resource, no increased level of exploitation was detected, and leaf consumption remained quite constant year round

(Figure 7-4). It seems that this resource is fairly heavily utilised, consisting of almost 25% of the diet by feeding bout frequency (Figure 7-1), but it is not a limiting resource. The fact that there was no correlation between use of young leaf and abundance of fruit (fruit and seeds), or seeds considered independently, further suggests that young leaf is not a fallback resource at the site that is, when abundance levels of other resources drop, leaf consumption is not increased to mitigate against this.

Overall, data presented here can not demonstrate that resource use is tracking availability (with the exception of flowers, which are seasonally exploited in line with availability), and the suggestion that seeds may be utilised at higher levels in the wet season. Additional work, including more data on a larger sample of plant species identified as preferred in this study, would be required to elucidate these relationships further.

There is however evidence to show that doucs at the site select dietary items in relation to daily energy requirements. It has been suggested that primates may specifically target high energy food sources such as fruits in the early morning in order to offset energy deficits built up over the previous night (Clutton-Brock, 1977). The impact of these energy deficits may be less on colobines than monogastric primates however, since fermentation is a more steady process which releases energy slowly over long periods of time (Davies, 1991).

From the current study, it appears that doucs in Seima Biodiversity Conservation Area are targeting high energy foods, specifically seeds, in the morning, presumably to offset energy deficits accrued over the preceding night. After this initial, and conspicuously frenzied, feeding bout, the doucs will settle down over the midday period, alternating between sleeping and casual consumption of food items close to hand, most usually leaves. The afternoons showed no clear trends in selection of specific food types for consumption.

Some comparative and complementary data relating to hourly feeding patterns exist for doucs. Hoang Minh Duc *et al.* (2009) found a penchant for doucs to consume fruit in the morning, as in this study, although they did not distinguish between fruit and seeds in their analysis. An opposite relationship was determined, based on very limited data (10 days of observation), from red-shanked doucs held in a 4 ha semi-wild enclosure at the Endangered Primate Rescue Center (EPRC). During this study there was an apparent

preference to target young leaves in the morning (Otto, 2005), although methods are not directly comparable with the current study or those of Hoang Minh Duc *et al.* (2009).

During the current study, different age and sex classes were also found to target different resources. Males spent less time feeding in general but also ate fewer leaves than females, tending to target seeds, while females fed extensively on immature leaves. This trend is also apparent in other studies. At EPRC, two male red-shanked doucs were found to consume less leaf matter, less petioles and less flowers than a female, while at Cologne Zoo female red-shanked doucs ate twice as many leaves as a male (Otto, 2005). Captive males also fed for less time than females at EPRC (Otto, 2005). How this apparent pattern may relate to metabolic requirements is beyond the scope of this thesis, but may provide an additional interesting line of research.

### ***What implications does diet have for species distribution, carrying capacity and conservation of *Pygathrix nigripes*?***

Generally food selectivity in primates has been measured fairly coarsely, using an index of feeding records to the frequency of that species within the habitat (e.g. Clutton-Brock, 1975, Julliot, 1996, Zhaoyuan Li *et al.*, 2003, Li and Rogers, 2005). Here I followed McKey and Gartlan (1981) in using basal area instead of stem number as it is not necessarily a plant species' frequency (i.e. the number of stems) but rather its mass that determines its productivity. Because of small sample sizes, and the fact that feeding records cannot be considered independent, only the species most commonly eaten and those most prevalent in the habitat will be discussed here.

Of interest when looking at Table 7-6 is that three of the top five species in terms of selection ratios come from the Fabaceae, all legumes that use atmospheric-nitrogen-fixing bacteria in root nodules as a key source of their plant nitrogen. Legumes clearly make up an important part of the diet of black-shanked doucs at the site, and appear to be specifically targeted, most often for their fruits and particularly their seeds. This high utilisation of legumes may be typical of doucs based on the small amount of information available. Wild black-shanked doucs at Nui Chua and Phuoc Binh NPs exploited legumes more than any other plant grouping (Hoang Minh Duc *et al.*, 2009). The highest number of species consumed from any family in the semi-free ranging doucs at the EPRC was from the Fabaceae (six species), and was also the second most popular plant family eaten in terms of time (Otto, 2005). For captives at EPRC, legume leaves made up 53% of all feeding time, and were the top four items in terms of time spent

eating (Otto, 2005). Exploitation of these leaves is possibly related to the fact that they are unligified, and therefore more digestible, and do not decrease in digestibility with increasing age (Van Soest, 1996), making them a good dietary option.

Of concern from a species conservation perspective may be the high use of the legume species *Azelia xylocarpa*, *Sindora siamensis* and *Peltophorum cf. dasyrrhachis*. These species are ranked four, five and one respectively for selectivity ratios, and all species are favoured targets of loggers. *Azelia xylocarpa* is of particular concern as it is utilised year round by the doucs, unlike the other two species, and may represent a fallback resource during periods of low resource abundance. The species is listed as Endangered (A1cd) on the IUCN Red List, and is a luxury timber species which is highly sought after in Cambodia, Vietnam and Thailand. It is a common victim of illegal timber harvesting and can attract prices of \$1200/m<sup>3</sup> (Global Witness, 2000). Both *Sindora siamensis* and *Peltophorum cf. dasyrrhachis* are listed as Royalty class 1 species in Cambodia, and are therefore prime targets for both legal and illegal loggers. Removal of these three apparently important species from forests containing black-shanked doucs may reduce carrying capacity and impact populations; as such conservation managers should be aware of their importance. Additional studies of densities related to legumes generally, and these three species specifically, are warranted.

The most highly selected non-legume species was *Irvingia malayana*, which also returned the highest frequency of feeding records. The high selectivity ratios and fraction of basal area from transects for *Irvingia malayana* may reflect the fact that this species is not targeted for exploitation by loggers. As a result, the site has a large number of large trees throughout, and these produce prodigious amounts of new leaf, flowers and fruit. The species is utilised throughout the year, with fruit, flower and young leaves all being targeted (see Table 7-5). As such, this species may represent one of the most important resources for sustaining the apparently high carrying capacity at the site (Pollard *et al.*, 2007) and may represent a keystone resource, that is, a resource which doucs may utilise during periods of scarcity (van Schaik *et al.*, 1993). This species was also fed upon extensively by black-shanked doucs at two sites in Vietnam (Hoang Minh Duc, 2007).

Species underutilised as food items by doucs tell an even more important story in regard to species distribution and potential carrying capacity. The most common species both in terms of number of stems and basal area at the site were *Lagerstroemia cf. calyculata*

and *Xylia xylocarpa*, together comprising almost 30% of all basal area on transects. These species also returned the lowest selectivity ratios of any species, with very few feeding records coming from either of them. As has been discussed in Chapter 4, they are the dominant species in mixed deciduous habitats which comprise a significant proportion of forests within the distribution of *P. nigripes*, not just in SBCA, but east into Vietnam (e.g. Cat Tien NP and Bi Dup-Nui Ba NR) and north through Cambodia.

This suggests that the transitional forests between the evergreen/semi-evergreen habitats which appear to hold high densities of black-shanked doucs, and the dry deciduous dipterocarp forests which apparently do not, may be a marginal habitat for them. This has implications for the potential carrying capacity of these forest types for the species. It was suggested in Chapter 6 that densities and group sizes of black-shanked doucs in *Lagerstroemia*-dominated forests may be lower, and the fact that this plant species is greatly underutilised as a food item, suggests a possible reason for this; lower available resource abundance in these habitats. While no analysis of the species' chemical and physical properties are available, the fruits are small and hard and contain winged seeds, and the laminae of its leaves are thick and waxy and are apparently unpalatable.

While black-shanked doucs may suffer lower carrying capacities in more marginal, non-evergreen forests, it appears that they can persist in very marginal environments. Nui Chua National Park, as noted above, represents a marginal environment with low rainfall, degraded forests with much of the area dominated by scrub and thorny trees (BirdLife International Vietnam Programme and The Forestry Inventory and Planning Institute, 2001). Dietary diversity at this site appears to be very high, with 135 plant species utilised compared to only 39 in Phuoc Binh NP (Hoang Minh Duc *et al.*, 2009) and 35 in the current study. The authors suggest this may relate to unequal survey effort at their sites, but the amount of observation time was 76 and 68 hours respectively, which would not seem to account for the very large discrepancy in records. It seems more likely that the difference is real, and the high number of species in the diet in Nui Chua may relate to marginal habitat quality and relatively high plant species diversity.

Oates (1977) noted that having a diverse diet may buffer an individual against increased toxicity from secondary compounds. Although I know of no literature relating to the phytochemistry of plants in Nui Chua NP, it seems likely that higher levels of secondary compounds would be present in such a water stressed environment compared to either Phuoc Binh NP or SBCA. The high relative diversity of exploited plant species in Nui

Chua NP may therefore represent an adaptation to avoid over consumption of harmful secondary compounds, which in turn may affect carrying capacity of the site.

Population estimates for Nui Chua NP are uncertain, ranging from 172 animals (Hoang Minh Duc and Ly Ngoc Sam, 2005) to 420-955 animals (Hoang Minh Duc *et al.*, 2004 in Hoang Minh Duc and Ly Ngoc Sam, 2005). Regardless, assuming a population of 955 animals and that most habitat types are utilised in the 15,000 ha of the park's core zone (Hoang Minh Duc and Ly Ngoc Sam, 2005), population density is very low (approximately seven animals/km<sup>2</sup>) when compared with SBCA (approximately 54 animals/km<sup>2</sup>) (Pollard *et al.*, 2007). This suggests that, hunting pressures aside, Nui Chua is a very marginal habitat for black-shanked doucs. No population data exist for Phuoc Binh NP, but it could be hypothesised that this site would have a considerably higher carrying capacity than Nui Chua NP based on the doucs' lower dietary diversity.

Another issue which may have implications for the species' distribution is the availability of water. SBCA, and indeed wherever the species occurs, has a marked dry season lasting four to six months between November and May with little or no rainfall. The species was not seen drinking water during this study. It has been found that the process of foregut fermentation of leaves used by colobines reduces the amount of water that has to be drunk as urea and urine production are reduced (Bauchop, 1978), so that colobines can go without water for long periods of time (McKenna, 1979). It has been suggested that this allows colobines to inhabit areas that are unavailable, at least seasonally, to other primates (Ripley, 1970).

The stresses of water debt force animals reliant on standing water (including long-tailed macaques at the study site) to congregate around water holes in the dry season, and predators may target these areas. Further, at these times competition would be increased in these areas, as there would be more individuals/unit area than in the wet season, which would impact on carrying capacity. Colobines, by avoiding a reliance on fixed water sources, can temporally and spatially utilise a wider area, reducing competition and thereby, incidentally, increase carrying capacity. This appears to be the case for doucs at the site, which are widely distributed year round.

Contrary to this is the fact that doucs reportedly drink large amounts of water in captivity (Hollihn, 1973, Ruempler, 1998), around 300-400 ml/animal/day at the EPRC (U. Streicher pers. comm.). Captive diets are generally comprised of food pellets or

dominated by leaf matter, and specifically by mature leaf matter. Large amounts of water are required to work highly absorbent mature leaf fibre through the digestive tract (Van Soest, 1996), suggesting that captive animals' consumption of large amounts of water may be related to diets. The recent record of a group of wild black-shanked doucs drinking standing water on a daily basis at one location in coastal Vietnam (Nadler, 2008) throws this into question, however. Whether doucs at SBCA utilise arboreal cisterns is unknown and was not documented. Additional research into the relationship between water consumption and diet in doucs is warranted.

## Summary

Data presented here suggest that black-shanked doucs in SBCA are best characterised as seed predators, with almost 40% of the diet composed of seeds. Doucs were also found to be highly selective in terms of food choice, with only 35 species of plant positively identified as food sources, the top five targeted species comprising 43.7% of all feeding observations and the top 15 plant species comprising over 71%. Preferred species, as determined by calculated selectivity indices, clearly show a preference for the Legumes, with three of the top five species coming from this plant grouping.

There was little indication that diets at the site tracked resource availability, based on resource abundance indices calculated from transect trees, the one exception being an increase in consumption of flowers as they became widely available just prior to the start of the wet season. Seasonal variation in seed consumption was also detected, with higher levels in the wet season, although this was not correlated with abundance (based on limited data). There was no seasonal variation in leaf consumption despite a large peak in availability in the dry season, and no suggestion that doucs need to fall back on leaves at certain times of year. Temporal daily trends in food type consumption were documented, with doucs showing a preference for consuming high energy seeds in the morning, possibly to offset night time energy deficits, and leaves in the mid afternoon.

Doucs in SBCA show a preference for plant species compositions found in evergreen and semi-evergreen forest. There was a clear trend to underselect dominant species associated with mixed deciduous forests, specifically *Lagerstroemia cf. calyculata* and *Xylia xylocarpa*. This suggests, along with other lines of evidence presented in Chapters 5 and 6, that mixed deciduous forest would have a lower carrying capacity. Despite this, it is apparent from other studies that doucs are able to incorporate a degree of flexibility in their diets, as in Nui Chua NP, although in these less optimal environments carrying

capacity may be reduced. Of some concern is that doucs rely heavily for their diet on very few tree species and these tree species are the targets of legal and illegal logging operations due to their high commercial value as timber. The impact of selective removal of these species on feeding ecology and douc carrying capacity is unknown but warrants further study.

## ***Conclusion***

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This thesis has examined the socio-ecology of *Pygathrix nigripes*, the black-shanked douc, focussing chiefly on habitat preferences, social behaviour and structure, and feeding ecology at a site in Seima Biodiversity Conservation Area (SBCA), Mondulhiri Province, Cambodia. The major findings and their implications are summarised in this chapter as well as priorities and opportunities for future research.

### **Habitat preferences**

In Chapter 4 of this thesis I described the four major habitat types at the study site and the key factors that define these typologies. The four forest types are evergreen, semi-evergreen, mixed deciduous and dry deciduous dipterocarp forest; these forest types form a continuum. Of particular interest in SBCA, and indeed across large amounts of the black-shanked doucs' distribution, are the habitat types generally referred to as semi-evergreen and mixed deciduous forest. While it is clear that these habitat types form a continuum, a forest patch's location on this continuum can best be identified by the relative density of *Lagerstroemia cf. calyculata* and to a lesser extent *Xylia xylocarpa*, these species being dominant in more mixed deciduous forests. Mixed deciduous forests, as well as having a higher percentage of deciduous trees, also tend to have lower species diversity.

Determining the suitability of these four forest types for *Pygathrix nigripes* was approached in a number of ways. Firstly, sightings of *P. nigripes* made by myself at the study site proper, and those made by Wildlife Conservation Society across SBCA, were usually accompanied by an assessment of the habitat type in which the sighting took place. These showed that black-shanked doucs occur in all four of the habitat types laid out above. Secondly, the relative frequency of encounters in each of these habitat types, based on data from 14 transects across the SBCA covering all habitat types, was assessed. This analysis showed that encounter rates of *P. nigripes* were positively correlated with evergreen forest and negatively correlated with dry deciduous dipterocarp forest; in other words that *P. nigripes* much preferred evergreen forest as a habitat. Thirdly, group sizes in different habitats was assessed following the rationale that sub-optimal habitats will hold fewer resources and therefore limit maximum group size, as hypothesised in the ecological constraints model. This showed that group size

was significantly smaller in areas dominated by dry deciduous dipterocarp forest compared to evergreen forest, but failed to differentiate any difference between either of these habitats and the intermediate habitat types of semi-evergreen and mixed deciduous forest.

While some of the analyses were hampered by the lack of a distinction in the GIS data set between mixed deciduous forest and semi-evergreen forest, and its probably insufficient resolution at the scale of analysis, basic patterns in habitat preference are clear. Dry deciduous dipterocarp forest is clearly sub-optimal habitat, returning lower encounter frequencies and smaller group sizes. It is likely that this habitat type is not used extensively because of its low plant species diversity, general lack of the plant species exploited by *P. nigripes* and low degree of canopy closure for a predominantly arboreal primate. It is also unlikely that this habitat type is utilised in areas where it is not associated with mixed deciduous and/or semi-evergreen habitats. *P. nigripes* clearly utilises mixed deciduous and semi-evergreen habitats extensively, but probably shows a preference for evergreen forest, returning higher densities and group sizes in this habitat type.

These analyses can be supplemented less directly through analysis of feeding ecology data. The list of plant species recorded as food resources for *P. nigripes* does not include those species most commonly found in dry deciduous dipterocarp forest, or show negative selection ratios. Strong negative selection ratios are also found for the dominant species located in mixed deciduous forests, specifically *Lagerstroemia cf. calyculata* and *Xylia xylocarpa*. These species make up a large proportion of basal area in mixed deciduous forests (they comprised 30% of total basal area on phenology transects in this study which also sampled semi-evergreen forest) and are apparently largely unpalatable for black-shanked doucs. By contrast, species that were commonly consumed and/or were overselected by *P. nigripes*, such as *Azelia xylocarpa*, *Sindora siamensis* and *Irvingia malayana*, are commonly found in semi-evergreen and evergreen habitats, further suggesting these habitats are the primary habitat types for the species within SBCA.

## **Behaviour**

From data presented in this thesis, it appears that *Pygathrix nigripes* has daily activity patterns similar to other colobine species studied to date. Activity begins at, or just prior to, sunrise and is quickly followed by intensive feeding for several hours. This is

followed by a long period which is dominated by resting with occasional social activities until mid-afternoon. At this time groups become more active again, seeking out feeding trees and travelling more than at other times of the day. This culminates in the late-afternoon, when groups move off to sleeping trees just prior to dusk. Sleeping trees may be selected based on their larger than average size and whether they are exploited for feeding.

Activity budget data showed that *P. nigripes* is inactive for a large proportion of the day, especially around the middle of the day, and that this usually occurs in the mid- to upper canopy on larger substrates. Feeding activity had a typically colobine bi-modal distribution, with feeding bouts in the morning and the afternoon. Locomotion was dominated by quadrupedal movement on larger substrates, with jumping the next most frequent mode, usually from more terminal branches, to facilitate movement between trees. Brachiation was a significant form of locomotion, although returned lower frequencies than captive studies on other *Pygathrix* species have suggested.

Social behaviour was infrequent, although typical for colobines, and included the affiliative intra-group behaviours of grooming and copulation and agonistic inter-group encounters. Grooming was predominantly performed by females and received predominantly by males and infants, suggesting that males are dominant within social groups. No instances of female-female grooming dyads were observed, suggesting dominance hierarchies amongst females are weak. Based on one observation, copulation is performed ventral-dorsal with multiple intromissions interspersed with reciprocated grooming and some aggression. While inter-group aggression was infrequent, it was significantly documented in two instances: firstly, between groups when attempting to access a key feeding resource, showing competition for resources does occur; and secondly, between the male of a one-male unit and those of a bachelor group, suggesting that male take-overs follow the typical pattern in colobines.

Several social activities not before observed in wild doucs were documented *ad libitum* during the current study, providing some insights that activity budgets fail to capture. Allomothering, as demonstrated by infant transfer, was observed closely on one occasion and inferred on several others. Paternalistic behaviour was also observed on one occasion, and is clearly within the behavioural repertoire of the species, although to what extent and under what conditions is still uncertain. An instance of peripheralisation

of a subadult male by the adult male of a one-male unit was recorded, suggesting that males, at least, disperse from their natal groups.

No overly significant seasonal variation or age and sex class differences in activity budgets were detected.

## **Social structure**

The social structure of *Pygathrix* has been discussed without much backing data for many years. It appears clear now that black-shanked doucs form four main social groupings: one-male units, lone males, all male bachelor groups, and bands which are comprised of two or more one-male units. During the study a few instances of larger “groups” with more than one adult male were observed, although it is unclear whether these were bands in which one-male units could not be readily distinguished or actually multi-male units, and so the possibility of a fifth social grouping does remain. Regardless, it appears that one-male units are the dominant social grouping, usually comprising one male, several females and offspring, averaging 7.5 individuals.

One-male units also coalesce into larger groups, typically called bands. The largest band recorded during the study was approximately 26 individuals, although there are reports of larger groups both at SBCA and in other locations. Bands often appear, during short observation periods, to be a single group, but when observations are of longer duration one-male units can be distinguished within the band, based on inter-individual proximity and cohesiveness in movement between individuals within the one-male units. Bands of black-shanked doucs undergo fission and fusion, similar to other odd-nosed colobines. This behaviour is apparently somewhat seasonal in nature, with larger groupings found in the wet season than in the dry season, coinciding with higher abundances of overselected plant resources. While it is clear that fission-fusion does occur in black-shanked doucs, the forces driving this process and the relationship between the one-male units involved remain unknown due to a lack of individual recognition during this study.

Additional males who, by virtue of the imbalance in one-male unit sex ratios, are not in breeding groups, either join bachelor groups or range alone. While lone males were frequently encountered, only one bachelor group was encountered during the study. However, this group, comprising some 17 individuals of all age classes except infants, appeared to have only one male with all secondary sex characteristics.

## Feeding ecology

Black-shanked doucs at SBCA were found to rely heavily on leaf matter, especially young leaves, and seeds, largely from Legumes. The finding that some 40% of the diet comprised seeds is an important discovery, and suggests that black-shanked doucs in SBCA are best characterised as seed predators. All other studies have suggested that doucs' diets are dominated by leaves, with low levels of seed or fruit consumption, although these studies have used a variety of different methods and have generally been of short duration.

The doucs in the study fed from only 35 species of positively identified plant species, a relatively small number and possibly a significant underestimate given the difficulty in getting identifications for many plant specimens. Although actual dietary diversity was probably higher than 35 species, it is clear that black-shanked doucs at the site were highly selective feeders, as the top five most consumed species comprised 43.7% of all feeding records. Given the plant species diversity within the environment, it is clear that some plant species are staple items, most notably *Irvingia malayana*, *Azelia xylocarpa* and *Peltophorum cf. dasyrrhachis*, the former two being exploited heavily for all plant organs and throughout the year. Based on this study and one in Vietnam (Hoang Minh Duc, 2007), which looked at plant species targeted by black-shanked doucs, it may be that some of these highly ranked plant species at SBCA are important across the species' range, specifically *Sindora siamensis* and *Irvingia malayana*. Presence and density of black-shanked doucs in relation to these and other key plant species distributions is a worthwhile topic for future studies, especially as some of these plant species are targeted by illegal and legal logging operations.

This study is the first to look at feeding ecology of doucs as it relates to resource availability. Generally, there was no indication that diets tracked resource availability at the site, with the exception of flower consumption. Flowers were consumed at high levels in association with high abundance levels just prior to the wet season. Seasonal changes in consumption were detected for seeds, with more seeds being consumed at higher levels in the wet season, although, based on limited data, this did not apparently track abundance of these resources. Doucs consumed high energy seeds preferentially in the mornings however, probably to offset night time energy deficits.

## Scope for future studies

The research conducted at SBCA Mondulkiri Province, and presented in this thesis lays the groundwork for additional study into black-shanked doucs and other species in the genus. This is the first study on the genus which has been conducted over a complete year and, as such, the baseline data presented here provide considerable opportunities to refine future research questions. Some future research questions I deem to be of importance are presented below:

How does fission-fusion work? While it is now clear that doucs, at least black-shanked doucs, live in fission-fusion societies, the mechanisms of band formation and separation are not understood. We do not understand the relationships between one-male units, nor under what circumstances and for what purpose they come together, although high resource abundance at certain times of year, as suggested here, may be hypothesised to facilitate fusion. Additional comparative work is also required for grey-shanked doucs and red-shanked doucs to determine whether fission-fusion occurs throughout the genus, the answer to which should be forthcoming as ongoing studies of these species reach fruition in coming years.

What is happening with sympatry and hybridisation? There are several sites where more than one species of douc have been recorded. As yet we have little to no understanding about how populations of different species interact in terms of niche partitioning and inter-breeding. Wild hybrids have been documented (Rawson and Roos, 2008), but the frequency of these occurrences, size of hybrid zones and viability of hybrids is unknown. Studies into these issues within these sites provide a good opportunity to better understand species distributions, hybrid species genesis and niche partitioning.

What are the impacts on population density and persistence of habitat degradation and removal of key plant species? While hunting represents the most significant threat to doucs across their range, the loss of habitat is a significant factor in the reduction of populations. I have suggested here that habitat quality influences douc group size, but additional research into the impact of selective removal of key plant species and general habitat degradation on population density and persistence are warranted. However, developing such a research project could be problematic given the confounding effects of hunting pressure.

Where are the key populations? While population data have been improving over recent years, there are still only a handful of sites where these data exist. Survey work to determine species strongholds needs to be conducted in order to allow for sensible prioritisation of populations for conservation interventions. Currently it seems that Cambodia is the species' only hope for large, genetically viable populations to exist into the medium to long term without significant population management; however significant additional survey work is required in Vietnam to determine whether this is truly the case. Targets for additional population surveys would include Bu Gia Map NP and Bi Doup-Nui Ba NR. Considerable effort also needs to be invested in standardising survey protocols and monitoring approaches, especially given the often fragmented nature of populations and the heavy threats they face.

Ultimately, all these research activities must fit within conservation-based initiatives. The black-shanked douc is currently listed as Endangered on the IUCN Red List (Rawson *et al.*, 2008), with many populations heavily impacted and few strongholds left. The red-shanked douc and grey-shanked douc are faring even worse. It is not only the long-term survival and viability of particular populations of this beautiful primate that are in question; the continuing existence of these species is at risk.



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## ***Tree species found on transects***

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<b>Family</b>	<b>Genus Species</b>	<b>n</b>
Anacardiaceae	<i>Mangifera</i> sp.	1
	<i>Semecarpus</i> sp.	2
	<i>Spondias pinnata</i>	1
Annonaceae	<i>Cananga latifolia</i>	2
	cf. <i>Enicosanthum</i>	1
	cf. <i>Polyalthia</i>	2
	<i>Xylopia</i> sp.	2
Apocynaceae	<i>Alstonia</i> sp.	5
	<i>Wrightia arborea</i>	3
Bignoniaceae	<i>Dolichandrone</i> sp.	3
	<i>Markhamia</i> cf. <i>stipulata</i>	12
	<i>Oroxylum indicum</i>	1
Bombacaceae	<i>Bombax anceps</i>	3
Celastraceae	cf. <i>Siphonodon</i>	4
Combretaceae	<i>Anogeissus acuminata</i>	9
	<i>Calycopteris floribunda</i>	6
	<i>Terminalia</i> sp.	8
Connaraceae	<i>Connarus paniculatus</i>	1
Datisceae	<i>Tetrameles nudiflora</i>	1
Dilleniaceae	<i>Dillenia</i> cf. <i>scabrella</i>	3
	<i>Dillenia</i> cf. <i>pentagyna</i>	1
Dipterocarpaceae	<i>Dipterocarpus</i> cf. <i>costatus</i>	9
	<i>Dipterocarpus alatus</i>	1
	<i>Dipterocarpus</i> cf. <i>intricatus</i>	1
Ebenaceae	<i>Diospyros</i> cf. <i>pilosanthera</i>	11
Euphorbiaceae	cf. <i>Cladogynos orientalis</i>	2
	cf. <i>Mallotus</i>	5
	<i>Baccaurea ramiflora</i>	2

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<b>Family</b>	<b>Genus Species</b>	<b>n</b>
Fabaceae	<i>Afzelia xylocarpa</i>	2
	<i>Albizia myriophylla</i>	2
	<i>Albizia cf. chinensis</i>	1
	<i>Bauhinia</i> sp.	7
	<i>Butea superba</i>	2
	<i>Dalbergia</i> sp.	2
	<i>Dalbergia oliveria</i>	4
	<i>Millettia</i> sp.	4
	<i>Millettia cf. pubinervis</i>	5
	<i>Peltophorum cf. dasyrrhachis</i>	1
	<i>Pterocarpus macrocarpus</i>	2
	<i>Sindora siamensis</i>	6
	<i>Xylocarpus xylocarpa</i>	26
Flacourtiaceae	<i>Hydnocarpus</i> sp.	6
Hypericaceae	<i>Cratoxylum cf. formosum</i>	6
Irvingiaceae	<i>Irvingia malayana</i>	6
Lamiaceae	<i>Vitex</i> sp1	4
	<i>Vitex</i> sp2	12
	<i>Vitex</i> sp3	19
Lauraceae	<i>Dehaasia suborbicularis</i>	3
	<i>Litsea</i> sp.	3
Lecythidaceae	<i>Careya arborea</i>	6
Loganiaceae	<i>Strychnos</i> sp	1
Lycopodiaceae	<i>cf. Lycopodiella cernua</i>	4
Lythraceae	<i>Lagerstroemia cf. calyculata</i>	49
	<i>Lagerstroemia</i> sp.	2
Moraceae	<i>Artocarpus rigidus</i>	1
Myrsinaceae	<i>Knema cf. erratica</i>	1
Myrtaceae	<i>Syzygium</i> sp.	4
Rhamnaceae	<i>Ziziphus cambodiana</i>	3
Rosaceae	<i>Parinari anamensis</i>	1

<b>Family</b>	<b>Genus Species</b>	<b>n</b>
Rubiaceae	<i>Haldina cordifolia</i>	1
Rutaceae	<i>Atalantia cf. monophylla</i>	1
Sapindaceae	<i>Dimocarpus longan longan</i>	1
	<i>Lepisanthes rubiginosa</i>	11
Staphylaeaceae	<i>Turpinia</i> sp.	1
Sterculiaceae	<i>Sterculia cf. urena</i>	1
Tiliaceae	<i>Microcos tomentosa</i>	35
Unknown	Unknown	81