# THE SOCIOECOLOGY OF WHITE-HEADED LANGURS (***Presbytis leucocephalus***) AND ITS IMPLICATIONS FOR THEIR CONSERVATION

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# Abstract

A study on the socioecology of white-headed langurs (*Presbytis leucocephalus*) was undertaken in Bapen Reserve, China, between December 1996 and September 1998. White-headed langurs occur on clumps of limestone hills in four counties in Southwest Guangxi. Due to the heavy pressure of human population, flat ground surrounding the groups of hills is largely lost to agricultural use and tree felling, thus the habitat of white-headed langurs is fragmented into several patches. In addition to habitat fragmentation, tree felling is another serious conservation issue that is often ignored in conservation management. White-headed langurs are endemic to this area thus it is necessary to investigate the effects of these human activities on their survival. The objective of this research was therefore to provide recommendations for improving the conservation management of white-headed langurs.

A survey was carried out on the overall population size in Bapen Reserve. Five groups of hills were surveyed. Data showed that local extinction has been occurring for a long time, due to habitat destruction and hunting. However, a drastic population decline has taken place over the past ten years. Most langurs were found in a hill-group in which the Reserve staff members often patrol. The langur population in this hill-group was defined as the main population pool of the Reserve. Further detailed sampling in the main population pool showed a much higher population density compared to other hill-groups. Langurs preferred large areas of continuous habitat. A similar survey was carried out in Longgang Reserve, Ningming County, which indicated a high population density in the central area of that reserve where the habitat has been much less disturbed by humans.

In the area of the main population pool, data were collected on climate, distribution of vegetation patches, plant species richness, phenology of food plant species, feeding ecology, range use and group dynamics of langurs. Habitat quality was classified according to the extent of human disturbance. Results showed that a large amount of mature leaves were available year round. Young leaves maintained a low level of availability, but disappeared almost completely in the winter of 1997. Rainfall was seasonal and was linked to the production of fruits and young leaves.

Vegetation was mainly distributed on the lowest 40% of the hills. Behavioural data showed that the activity of white-headed langurs was restricted to the hills by the distribution of vegetation.

Langurs fed mostly on less common plant species. These were more likely to occur in the higher quality habitat, for which different langur groups competed. As a consequence, only the langur groups living in 50% of the higher quality habitat area produced offspring. Langurs fed intensively on young leaves. Compared to other colobine species, white-headed langurs were extremely folivorous.

The home ranges of langur groups were smaller in higher quality habitat and well defended. Adult males seemed to compete for habitat to attract females. Inter-group spacing was maintained by loud calls accompanied by jumping about by breeding males. A bisexual group was composed of one adult male, several adult females, and their offspring. In the main study area of this research, only a few males made a genetic contribution to the next generation in the observation period from September 1997 to September 1998. With further habitat degradation, the number of breeding males may decrease further, which may accelerate extinction of the whole population of langurs in Bapen Reserve.

Based on these findings and conservation issues in Bapen Reserve, some recommendations are provided for improving langur conservation management. The goal is to avoid extinction of the Bapen population of langurs in the foreseeable future. Options for *in situ* and *ex situ* conservation action are recommended. *In situ* action is classified into three phases: short-term action is to stop the current trend of population extinction and habitat degradation immediately. Medium term action is to increase the area of high quality habitat, and then allow the langur population to recover. In addition to white-headed langurs, other wild plants and animals will also benefit from these objectives.

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Chapter I

# INTRODUCTION

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## 1.1 Evolution of Colobine Monkeys

The earliest primates evolved from an insectivorous mammal in the latest part of the Cretaceous period or the early Palaeocene (Fleagle, 1988, 1999), about 65-70 million years before present (M.Y.B.P.). It is impossible to determine the exact relationship of primates and other mammals, but studies on palaeontology, comparative anatomy, and molecular biology indicate a close relationship of modern primates and tree shrews, flying lemurs, and bats (Wible & Covert, 1987; MacPhee, 1993). The first modern primates appeared in the Eocene (Simons, 1972; Fleagle, 1999), showing all the anatomical features characteristic of living primates, such as shorter snouts, smaller infraorbital foramina, and a postorbital bar completing the bony ring around their orbits (Fleagle, 1999). The Hominoidea diverged from other primates in the Oligocene (Szalay & Delson, 1979), about 33 M.Y.B.P. The ancestry of the families Colobinae and Cercopithecinae is traceable to early catarrhines similar to the Fayum propliopithecids (Delson, 1975; Szalay & Delson, 1979; Fleagle, 1988). The oldest members are *Prohylobates* and *Victoriapithecus* (early Miocene, 20-15 M.Y.B.P.) (Delson, 1994). These two families diverged in the late Miocene, about 11 M.Y.B.P. (based on fossil records, see Peng & Ye,1987) to 15 M.Y.B.P. (based on the study of cytochrome b, see Fleagle, 1999). At about 12.5 M.Y.B.P., modern African and Asian colobine monkeys started to diverge (Fleagle, 1999).

Fossil colobine monkeys occurring in Africa (mainly in Early Miocene and Pliocene deposits, 23-1.8 M.Y.B.P.) are in general older than in Asia (mainly in Pleistocene deposits, 1.8-0.13 M.Y.B.P.), and the age is intermediate in Europe and the Middle East (mainly in deposits from later Late Miocene to Later Pliocene, 8.5-1.8 M.Y.B.P.) (Delson, 1994). This leads to a direct impression that colobine monkeys dispersed from the West (Africa and Europe) through the Middle East to Asia, and it is further proposed that there was a centre for *Presbytis* speciation in the

India-Pakistan subcontinent (Peng & Ye, 1987). Species originating from this centre further dispersed eastward to East and Southeast Asia. A difficulty rising from this hypothesis is the explanation of by what substrate these colobine monkeys dispersed. Buettner-Janusch (1963) imagined an ancient forest corridor connecting Africa and Asia, because folivorous colobines are found in both continents. The fossil *Mesopithecus pentelicus,* discovered in open grassland in Greece, was adapted to terrestrial life but cranially similar to arboreal colobine monkeys. Simons (1972) argued that a continuous forest corridor was impossible from Central Africa to Southeast Asia and that the colobine monkeys reaching Southeast Asia must have been terrestrial. Delson (1994) held a similar point of view. The earliest well-known colobine, *M. pentelicus,* was not African but Eurasian, and the earliest fossil in China was found in a deposit of the later Late Miocene (Delson, 1994), similar in age to *Presbytis silvalensis* (8 M.Y.B.P.), the oldest fossil in the centre for speciation in the subcontinent. This indicates that the ancestry of Colobinae (*Mesopithecus,* Radinsky, 1975; Szalay & Delson, 1979) was a form that spread widely from Africa and Europe to Asia, the distribution of which was consistent with the occurrence of open steppes with some patches of forest from Greece (Delson, 1994) to China (Wu & Li, 1994). Based on morphological and anatomical studies, Peng & Ye (1987) proposed that the genera *Presbytis* and *Rhinopithecus* are two descendants of *Mesopithecus*. Wu & Li (1994) further proposed that *Rhinopithecus* evolved locally during habitat change caused by the active Quaternary tectonic movement. There is debate on when the Asian colobines shared a common ancestry (Oates *et al.*, 1994). Delson (1994) places their ancestor in the middle Pliocene. According to Groves (1989), *Nasalis* (with *Simias*) is paralleled with all other colobines through sharing a set of retained primitive features. In other words, *Nasalis* (with *Simias*) in Asia separated from other colobines earlier than African and Asian colobines diverged.

In evolutionary history, there were diverse colobine monkeys in Africa, but because of regional climatic change and perhaps the rise of competition from cercopithecines, the diversity reduced afterward (Delson, 1994). Jablonski & Tyler (1999) report that Javan lutung (*Trachypithecus auratus sangiranensis*, 1.9±0.05 M.Y.B.P.) is one of the oldest fossil monkeys from eastern Asia. Colobine variety increased in eastern Asia during the Pleistocene, which continues till now, and the reason is not yet known. There are some 30 living colobine species, most of which are found in Asia (Oates *et al.*, 1994).

## 1.2 Classification of Colobine Monkeys in Asia

### 1.2.1 Brief review

Elliot (1913) first proposed the family Colobidae (also see Groves, 1989), which, along with the family Cercopithecidae, is placed under the superfamily Cercopithecoidea (Peng, 1987). Colobine monkeys are also placed as a subfamily of the family Cercopithecidae in the classification system of other authors (Napier & Napier, 1985; Fleagle, 1988, 1999). In the former system, the family is not divided into subfamilies (Peng, 1987), simply including genera, or the family includes two subfamilies, Nasalinae and Colobinae (Groves, 1989).

Colobine monkeys are often arranged in two clusters, one African and one Asian (Oates *et al.*, 1994). The African cluster contains only the genus *Colobus* (Napier & Napier, 1967; Peng, 1987), including some 3 (Buettner-Janusch, 1963; Walker, 1968), 5 or 6 species (Napier & Napier, 1967), or two genera, *Colobus* and *Procolobus,* including 6 (Fleagle, 1988, 1999) or 7 species (Napier & Napier, 1985; Oates *et al.*, 1994). The Asian cluster is much more diverse, containing 5 (Napier & Napier, 1985; Peng, 1987; Fleagle, 1988), 6 (Oates *et al.*, 1994), or 8 genera (Fleagle, 1999). *Table 1- 1* shows a summary. It is shown that Asian colobines are less clearly united than the African colobines. The classification is in dispute especially that of the langurs.

### 1.2.2 Classification of Asian langurs

The division of *Presbytis* into several genera or subgenera has had a long history. Reichenbach (1862, cited in Oates *et al.*, 1994) recognised four subgenera for Asian langurs. Pocock (1939) classified all langur species found in Sumatra, Borneo,

Table 1-1 Classification of colobine monkeys

| Superfamily | Family | Subfamily | Genera | Source |
|---|---|---|---|---|
| Cercopithecoidea | Cercopithecidae | Colobinae | (1), (2), (4), (5), (6), (7), (8) | Napier & Napier 1985 |
| | | | (1), (2), (3), (4), (5), (6), (7), (8), | Fleagle 1988 |
| | Cercopithecidae | Colobinae | (1), (2), (3), 4 genera for langurs, (5), (6), (7), (8) | Fleagle 1999 |
| | Colobidae | Nasalinae | (7), (8) | Groves 1989 |
| | | Colobinae | other genera | |
| | | | (1), (2) (*Piliocolobus* included), (5) (*Rhinopithecus* included), (7), (8), 3 genera for langurs | Oates *et al.* 1994 |
| Cercopithecoidea | Colobidae | | (1) (*Procolobus* and *Piliocolobus* included), (4), (5), (6), (7), (8) | Peng 1987 |

(1) *Colobus,* black colobus and black and white colobus; (2) *Procolobus,* olive colobus; (3) *Piliocolobus,* red colobus; (4) *Presbytis,* langurs; (5) *Pygathrix,* douc langurs; (6) *Rhinopithecus,* snub-nosed monkeys; (7) *Nasalis,* proboscis monkeys; and (8) *Simias,* pig-tailed leaf-monkeys.

Malaya, and Burma in the genus *Presbytis.* Ellerman & Morrison-Scott (1951) used this genus to include all langur species in Asia. Hooijer (1962) divided langur species in Indonesia into two genera: *Presbytis* and *Trachypithecus,* because these two groups are different in morphology (Groves, 1970). In morphology, Indian langurs that were classified into *Semnopithecus* and *Kasi* by Hill (1936) are intermediate between these two groups (Groves, 1970). A well-known classification (Napier & Napier, 1967) was widely accepted at least in the behavioural literature in the 1970s and most of the 1980s, in which *Presbytis* was accepted to be the generic name of all Asian langur species. Brandon-Jones (1984) proposed to arrange these langur species into *Presbytis* and *Semnopithecus,* with *Trachypithecus* included in the latter genus, which was followed by Strasser & Delson (1987). Fleagle (1988) recognised the differences in morphology and ecology among these langur species groups and assigned three subgenera in *Presbytis*; they were *Semnopithecus* (including *entellus, senex,* and *johnii*), *Presbytis* (including *aygula*, *melalophos, rubicunda, thomasi, potenziani, frontata*, and *hosei*), and *Trachypithecus* (including *obscura, phayrei, cristata, pileata, geei,* and *françoisi*). This assignment is now upgraded to generic level, in which one more genus is added (Fleagle, 1999). These genera are *Semnopithecus* (including only *entellus*), *Kasi* (including *vetulus* and *johnii*), *Trachypithecus* (including *obscura*, *phayrei, cristata, auratus, pileatus, geei*, and *françoisi*), and *Presbytis* (including *melalophos, comata, rubicunda, frontata, thomasi, hosei*, and *potenziani*). Oates *et al.* (1994) accepted a three-genus arrangement, in which the two species in Fleagle's *Kasi* were included in *Trachypithecus*. These three genera are different in infant pelage coloration, feeding ecology and locomotion behaviour. Hanuman langurs (*Semnopithecus*) are the most terrestrial of the colobines (Fleagle, 1999). They move largely in quadrupedal gaits. They eat fruit, flowers, and new leaves and seem unable to subsist on a diet of mature leaves. By their blackish-brown coat coloration, new-born hanuman langurs are different from *Trachypithecus* infants whose coloration is orange or brown, and from *Presbytis* whose new-borns are white or whitish (Oates *et al.*, 1994). *Trachypithecus* is more folivorous and *Presbytis* more frugivorous, and *Semnopithecus* is intermediate between them in feeding ecology (Bennett & Davies, 1994). Compared to *Trachypithecus*, *Presbytis* are more arboreal (Fleagle, 1976; Strasser, 1992). These taxonomic groups are also different in habitat types. The subgenus *Trachypithecus* tends to be more likely present in deciduous and semi-deciduous forests, *Presbytis* in evergreen forests, and *Semnopithecus* in open habitat. In this thesis, I tentatively follow Fleagle (1988) with regard to the differences at sub-generic level and Oates *et al.* (1994) with regard to subdivision of the genus *Presbytis* into three subgenera: *Semnopithecus*, *Trachypithecus*, and *Presbytis*. This classification is also discussed using data from this study in Chapters IV, V, and VI.

There were 14 species recorded for the genus *Presbytis,* including 84 (Napier & Napier, 1967; Walker, 1968; Peng, 1987) or 60 subspecies (Buettner-Janusch, 1963). With more detailed studies, the species inventory changes often. For example, *vetulus* is now used to replace *senex* (Oates *et al.*, 1994), because the original description was based on an albino monkey from an unknown locality (Napier, 1985). *P. aygula* is not valid due to the rules of nomenclature (Weitzel & Groves, 1985) and is replaced by *P. comata* (Napier & Napier, 1985; Oates *et al.*, 1994; Fleagle, 1999). Two subspecies, *P. c. hosei* and *P. c. thomasi* have emerged as full species (Napier & Napier, 1985; Fleagle, 1999). *P. cristata auratus* is upgraded to a full species (Oates *et al.*, 1994; Fleagle, 1999). In Oates *et al.* (1994) and Fleagle (1999), 17 langur species are recognised, which is accepted in this thesis. *Table 1- 2* summarises the classification that I tentatively follow. In the present study, ***langur*** is used both to indicate broadly all species in the genus *Presbytis* and specifically the species of the subgenus *Trachypithecus*. In the former case, this name is used without limitation (for example, *langur species* refers to any species in the genus). In the latter case, this name is used with another specific name for the species (for example, *dusky langur* refers to the species *Presbytis (T.) obscurus*).

Five subspecies were recognised in François' langur, including the nominate *françoisi, delacouri, laotum, poliocephalus*, and *leucocephalus* (Buettner-Janusch, 1963; Napier & Napier, 1967; Walker, 1968; Li & Ma, 1980). The classification is still in dispute and has attracted the interest of primatologists working on genetics and field biology (T. Nadler and C. Roos, *pers. comm.*) Because these geographical

Table 1-2 The species of living langurs*

| Latin name | Common name |
|---|---|
| *Presbytis (Presbytis) melalophos* (Wurmb, 1821) | Banded leaf-monkey |
| *Presbytis (Presbytis) comata* (Desmarest, 1822) | Javan leaf-monkey |
| *Presbytis (Presbytis) frontata* (Müller, 1838) | White-fronted leaf-monkey |
| *Presbytis (Presbytis) rubicunda* (Müller, 1838) | Red (or maroon) leaf-monkey |
| *Presbytis (Presbytis) potenziani* (Bonaparte, 1856) | Mentawai leaf-monkey |
| *Presbytis (Presbytis) hosei* (Thomas, 1889) | Hose's leaf-monkey |
| *Presbytis (Presbytis) thomasi* (Collett, 1893) | Thomas' leaf-monkey |
| *Presbytis (Trachypithecus) vetulus* (Erxleben, 1777) | Purple-faced langur |
| *Presbytis (Trachypithecus) auratus* (E. Geoffroy, 1812) | Lutung |
| *Presbytis (Trachypithecus) cristatus* (Raffles, 1821) | Silvered langur |
| *Presbytis (Trachypithecus) johnii* (Fischer, 1829) | Nilgiri langur |
| *Presbytis (Trachypithecus) obscurus* (Reid, 1837) | Dusky langur |
| *Presbytis (Trachypithecus) pileatus* (Blyth, 1843) | Capped langur |
| *Presbytis (Trachypithecus) phayrei* (Blyth, 1847) | Phayre's langur |
| *Presbytis (Trachypithecus) françoisi* (Pousargues, 1898) | François's langur |
| *Presbytis (Trachypithecus) leucocephalus* (T'an, 1957) | White-headed langur |
| *Presbytis (Trachypithecus) geei* (Gee, 1956) | Golden langur |
| *Presbytis (Semnopithecus) entellus* (Dufresne, 1797) | Hanuman or grey langur |

* The word Langur is used to indicate all species in the genus *Presbytis*.

races are regarded either as species or subspecies, they are given a neutral term ***françoisi group*** (V. Weitzel, *pers. comm.*)

### 1.2.3 Classification of *françoisi* group

There are six races that were classified as subspecies of *Presbytis françoisi* (Peng, 1987). These are *P. f. françoisi, P. f. delacouri, P. f. laotum, P. f. poliocephalus,* and *P. f. leucocephalus*. Only the nominate subspecies *P. f. françoisi* exists in large numbers (Wu, 1983; Weitzel, 1992; Weitzel & Thanh, 1992) and others are endangered due to small population size and distribution range (Wu, 1983; Weitzel & Thanh, 1992; Ruggeri & Timmins, 1996; Li *et al.*, 2000).

According to this classification, *P. françoisi* shows significant racial variation in pelage (Weitzel, 1992). *Françoisi* and *leucocephalus* seem to be at two extremes in fur coloration. *Françoisi* is black all over in fur coloration, whereas *leucocephalus* has a white tail (proportion of white part variable) and a white head. *Poliocephalus* has a white head and a black tail, which is intermediate (Plate 1- 1). Due to this difference, *leucocephalus* was regarded as a species when it was first reported (T'an, 1957), but because of similarities in cranial morphological measures, it was later regarded as a subspecies of *P. françoisi* (Li & Ma, 1980). Li & Ma claimed that they had found hybrids with a white head and a black tail, which sounds like a *poliocephalus*. According to field observation (*pers. obs.*), hybridisation is impossible in the present environment, because habitat fragmentation has isolated langur populations from each other (about 2km within white-headed langurs and tens of kilometers between white-headed and François' langurs). Between these populations are agricultural land, human settlements, rivers, and highways. Lu & Li (1991) compared the similarity of these two forms in ecology, proposing that competition for similar resources may be the reason for their separation, which hints at the possibility of different species. This paper was incorrectly cited by Burton *et al.* (1995), saying that results from this paper were in conflict with Li (1993b). Wang *et al.* (1997) reported genetic data, showing that the genetic distance was closer between *leucocephalus* and *françoisi* than that between *françoisi* and *P. phayrei*, based on which they supported the status of *françoisi* and *leucocephalus* as two

**Plate 1- 1 A comparison among *françoisi*, *leucocephalus*, and *poliocephalus*, showing the difference in pelage coloration.**

(a) *françoisi,* (b) *leucocephalus*, and (c) *poliocephalus.* (*Poliocephalus* photographed by T. Nadler, and others by the author) subspecies. However, because no objective criterion was given for measuring genetic distances between species and subspecies in this paper, the data were no more precise than those on morphology in resolving their classification. Brandon-Jones (1984) regarded *françoisi, leucocephalus* and *delacouri* as full species on the basis of pelage differences. He also listed *poliocephalus* as a subspecies of Nilgiri langurs (*P. T. johnii*) in South India, which was rejected by Oates *et al.* (1994).

It is hard to believe that *poliocephalus* and *leucocephalus* belong to the same race due to the distribution pattern of white-headed and François' langurs in South China (detailed below). White-headed langurs are found in an area surrounded by the Mingjiang River, Zuojiang River, and Shiwandashan Mountains. Between *leucocephalus* and *poliocephalus* are François' langurs, so the possible continuous distribution from *leucocephalus* to *poliocephalus* does not seem to exist. Meanwhile, the two rivers and the mountains did not seem to prevent interchange between *leucocephalus* and *françoisi* before vegetation clearance, in terms of the mountain height and the history of development of the rivers (Lu & Li, 1991), but they are not sympatric in distribution, indicating the possible result of competitive exclusion. In *Table 1- 2*, I tentatively accept the classification at species level of Oates *et al.* (1994) for all these subspecies, except for *leucocephalus*. The white-headed langur has been tentatively separated from François' langur.

## 1.3 Distribution of Colobine Monkeys in Asia

### 1.3.1 Brief review

Asia contains a wide variety of forest types from tropical evergreen rain-forests to montane, temperate and highly seasonal forests. They are largely determined by climate, though other factors also impose additional influences on them, such as soil, altitude and human disturbance (Bennett & Davies, 1994). All the study sites in Asia (see *Figure 1- 1*) are affected by at least one of two monsoons: from the south-west in June-July and from the north-east in December-January.

Rainfall increases from the north to the south in India. The south-west monsoon brings 1600 – 1700mm of annual rainfall to Simla (3500m a.s.l., South

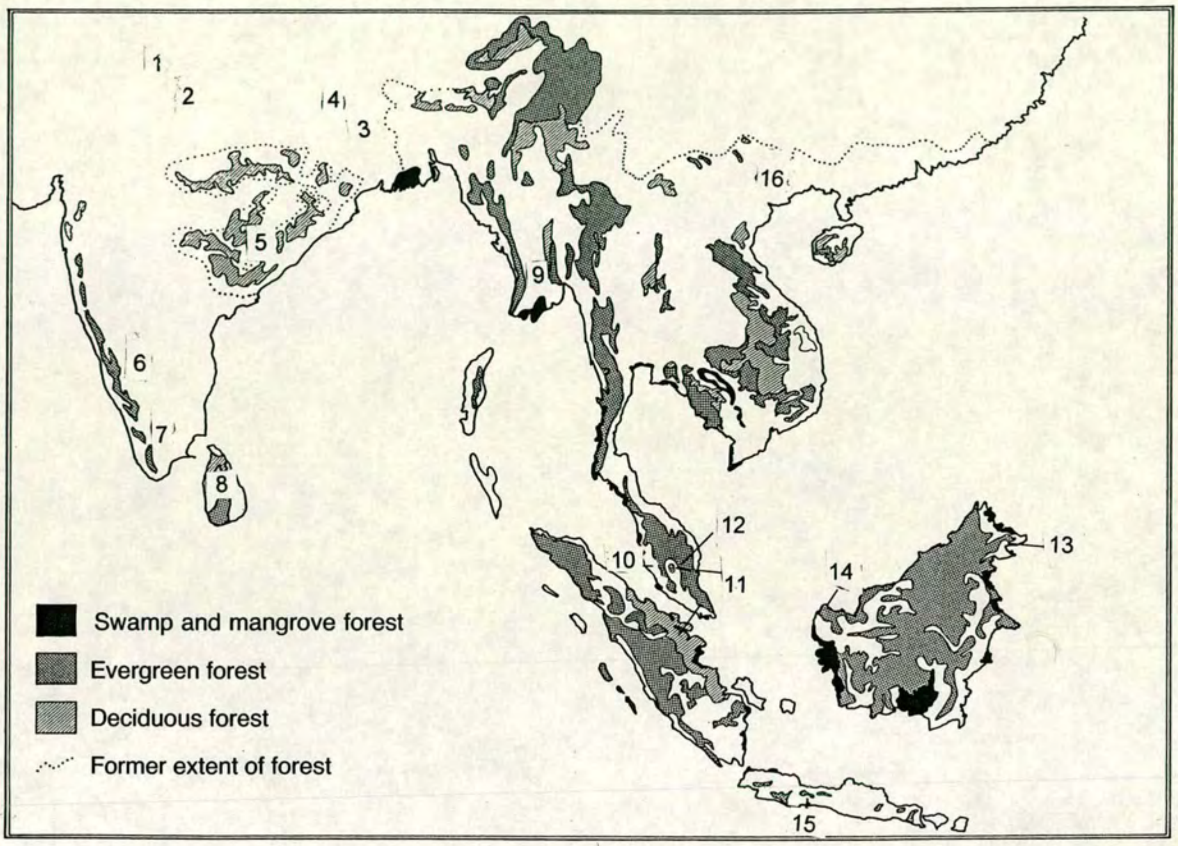


**Figure 1- 1 Distribution of evergreen, deciduous and swamp forests in Asia, and localities of colobine socio-ecology study sites (from Figure 5.1, Bennett & Davies, 1994, modified). Sites: 1. Simla; 2. Bhimtal; 3. Junbesi; 4. Melemchi; 5. Kanha; 6. Periyar; 7. Kakachi; 8. Polonnaruwa; 9. Madhupur; 10. Kuala Selangor; 11. Kuala Lompat; 12. Sungai Tekam; 13. Sepilok; 14. Samunsam; 15. Pangandaran; 16. Bapen.**

India) and Kanha (the Indian central highlands) (Sugiyama, 1976; Newton, 1988). The annual rainfall at Kakachi (South India) increases as high as 3080mm, which is brought by the two monsoons (Oates *et al.*, 1980). Further south to Polonnaruwa, Sri Lanka, however, because of the uplands blocking humid air from the south-west, most of the 1670mm of annual rainfall is brought by the north-east monsoon from the Bay of Bengal. South-east Asia tends to have more precipitation than India and Sri Lanka, but follows a similar climatic pattern. Sepilok (Borneo) receives an annual rainfall of 3000mm in the first peak of rain in December that is sometimes followed by a secondary peak of rain in June. Kuala Lompat (Malaysia) is between two hill ranges that block moisture brought by both monsoons. As a result, this area receives much less rainfall (2000mm), compared to other sites nearby, with a tendency to be heavier during the north-east monsoon (Raemaekers *et al.*, 1980). In south China at the north, Bapen receives least rainfall (the rainfall of Fusui county, in which the study site locates, is only 1245mm) among all Asian study sites (detailed in Chapter II).

The highest rainfall supports the greatest tree-species richness in the dipterocarp forests of South-east Asia (Whitmore, 1984; Bennett & Davies, 1994). At Sepilok, about 160 tree species > 10cm dbh were found in an area of 1.25 ha and 180 species > 6cm dbh found in 2 ha at Kuala Lompat; in contrast, some 30 tree species > 5m tall were found in 2 ha in Polonnaruwa and about 25 species > 2m tall in the same survey size at Kanha (Dittus, 1977; Raemaekers *et al.*, 1980; Davies, 1984). This tree species richness is related to the complicated structure of the forests in South-east Asia (Bennett & Davies, 1994). Some emergent trees grow 80m high, standing head and shoulders above the main canopy trees. Beneath are the dense understory trees and saplings. This structure provides substrate for primates at multiple levels. In the drier semi-deciduous forest, some species dominate the forest (*Drypetes sepiara* in Polonnaruwa and *Shorea robusta* in Kanha); but in the wetter tropical evergreen forest, there are no dominant species. This means that colobine monkeys in evergreen forests have more food plant species than in deciduous environments, and the choice is greatest in the south-east Asian dipterocarp forests.

The extent of seasonality decreases with the diversity of species that have different timing in their phenological cycle. This does not exclude the important influence of climatic pattern. Leaf production is far more seasonal in the drier forests of South Asia (only a single peak of young-leaf production per year) than the wetter forests of South-east Asia (two peaks of young-leaf production that provide substantial young leaves and abundant mature leaves year round) (Raemaekers *et al.*, 1980; Bennett, 1983; Davies, 1984; Bennett & Davies, 1994). This may be the reason why there is the greatest species richness of colobine monkeys in South-east Asia.

Colobine monkeys are widely distributed from Kashmir and Nepal through Burma and China, and southwards through the Indian subcontinent, Indo-China and Malaya to Sumatra, Java and Borneo. The altitude above sea level ranges from a few meters (Proboscis monkeys in mangrove forest) to 4,300m (Yunnan snub-nosed monkey in Southwest China). Their habitat types include Dry zones of India and Sri Lanka, snow-covered habitats and rocky outcrops in the Himalayas, mangrove swamps and rain forest (*Figure 1- 1*).

Of the five genera (see above), the genus *Presbytis* has the largest distribution range and occupies almost the whole ecological range. *Rhinopithecus* species are found in the provinces of Sichuan, Gansu, Shaanxi, Hubei, Guizhou, and Yunnan in China, and in North Vietnam (Liu, 1959; Song, 1959; Zhao, 1959; Hu *et al.*, 1980; Deng, 1981; Li, 1981; Xie, 1981; Nhat, 1994). Their populations have been restricted to isolated mountains (see *Figure 1- 2*). Of the four species in this genus, the Sichuan golden monkey (*R. roxellanae*) has the largest distribution range on Qinling Mountains. This species occurs in mixed broadleaf-conifer and pure conifer forests between 1800 - 2800m above sea level (a.s.l.) (winter) and 3000 -3300m (summer) (Schaller, 1985; Schaller *et al.*, 1985; Happel & Cheek, 1986). The vertical migration is related to the severe climate this species experiences (Bennett & Davies, 1994), with snow cover for about 6 months of the year and frost for 280 days per year. The Yunnan snub-nosed monkey (*R. bieti*) has the highest distribution range between 3000 and 4300m a.s.l. (Long *et al.*, 1994), but this species does not show vertical migration between summer and winter, which is different from Sichuan golden monkeys. It occurs in association with fir-larch forests. Guizhou snub-nosed

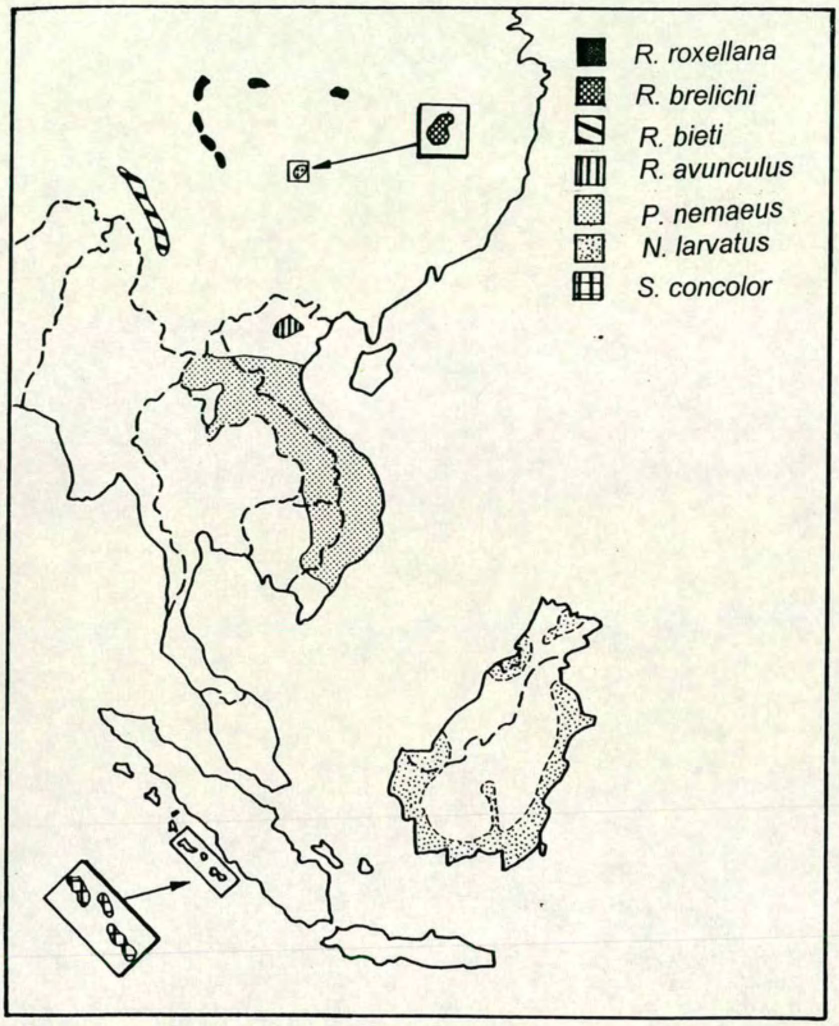


**Figure 1- 2 Distribution of the genera *Rhinopithecus, Pygathrix, Nasalis*, and *Simias* (from Figure 3.5, Oates *et al.*, 1994)**

monkeys (*R. brelichi*) occur in the mixed evergreen-deciduous broadleaf forests between 1500 and 2200m a.s.l. on Fanjingshan Mountains (Bleisch *et al.*, 1993). *R. avunculus* in northern Vietnam is confined to forest over limestone, perhaps due to habitat loss (see MacKinnon, 1986).

*Pygathrix* has a large distribution in the Indo-China region (see *Figure 1- 2* ), covering most of the area of Vietnam, the whole of Laos, and nearly 1/3 of Cambodia. On Mount Sontra in Vietnam, douc monkeys occur in mixed and partly deciduous moist forests (Lippold, 1977). *Nasalis* share their coastal swamp and riverine forests with *Presbytis (T.) cristatus* (see *Figure 1- 2*). They are found in mangrove-nipa forest over this lowland (Bennett & Sebastian, 1988). In Sarawak, they also live in a mixture of heath and lowland dipterocarp forests away from the Samunsam River. Plant species biodiversity in mangrove forest is very low (Anderson, 1980), which, combined with the scarcity of foods, might explain why proboscis monkeys frequently use both mangrove and riverine forest (Bennett & Davies, 1994); *i.e.*, these two habitats likely provide them a greater variety of food sources throughout the year. At Samunsam, proboscis monkey groups commonly spent more time feeding on young leaves in mangrove forest when fruit in the riverine forest was scarce (Bennett & Sebastian, 1988).

*Simias* coexists together with *Presbytis (P.) potenziani* on the Mentawai islands (see *Figure 1- 2*). They are found in the forests growing on poor soils and containing a high proportion of dipterocarps (*e.g.*, 21% at Paitan, a field site on Siberut, the largest of the Mentawai Islands, (Whitten, 1982). *Simias* is an endemic genus and *P. (P.) potenziani* an endemic species to these islands.

Compared to the above genera, the genus *Presbytis* has covered a much larger area, the northern limit of which reaches to Kashmir (*P. entellus*), the southern to Java (*P. comata*), and the western as far as the north of Pakistan (*P. entellus*). This area includes altitude ranging from 0 (Paitan where *P. potenziani* occurs and Sepilok where *P. rubicunda* and *P. hosei* are distributed) to 3000m a.s.l. (Junbesi in east India where Hanuman langurs occur). Several different habitat types occur in this area.

### 1.3.2 Distribution of *Presbytis* species

(a) *The subgenus Semnopithecus*: This subgenus occurs on the south slopes of the Himalayas, including most of India, Sri Lanka, Nepal, Sikkim, south Kashmir, north Pakistan, Bangladesh, a small part of Bhutan, and south Tibet in China (see *Figure 1-3*). Animals of this subgenus are found from sea level to an altitude of 4000m, and in a great range of habitats from dry tropical scrub jungle to montane coniferous forest (Roonwal & Mohnot, 1977). They do not inhabit closed-canopy tropical forests, but exhibit considerable terrestriality (Oates *et al.*, 1994). Only the Hanuman langurs can survive between the Western Ghats and Assam, because the deciduous forests in this area are not suitable habitat for other colobines that dwell in evergreen forest. Due to the monkey-god Hanuman in Hindu mythology (Hrdy, 1977), they are tolerated by humans and are found in human settlements.

(b) *The subgenus Trachypithecus* occurs in south China, the Indo-china region, Burma, Bangladesh, Bhutan, Assam in India, south India, Sri Lanka, Thailand, the Malayan Peninsula, and the Sunda Islands (*Figure 1- 4*). Compared to the subgenus *Presbytis, Trachypithecus* species occur in a wider range of environments, including moist and wet lowland forests, dry deciduous forest, coastal mangrove swamps, and montane broad-leaved forests. The Nilgiri langur (*P. (T.) johnii*) is restricted to the Western Ghats of southern India. It occurs in the Shola forests of the southern hills above altitudes of 500 to 600m a.s.l., and also in some of the lush gallery forests which extend into the drier woodlands below (Poirier, 1970). Its close relative, the purple-faced langur (*P. (T.) vetulus*), occurs in Sri Lanka and replaces the Hanuman langur in the wetter evergreen forests of southern Sri Lanka. In the intermediate semi-evergreen forests of central Sri Lanka, *P. vetulas* and *P. entellus* are sympatric. These forests are characterised by two tree layers; the upper tree layer is deciduous during the dry season and the lower layer remains evergreen (Dittus, 1977).

*P. (S.) entellus* is replaced by *P. (T.) geei* in Assam where the forests mark the eastern limit of the distribution of the Hanuman langur and the western boundary of the most diverse array of colobines in the world (Bennett & Davies, 1994). *P. geei*

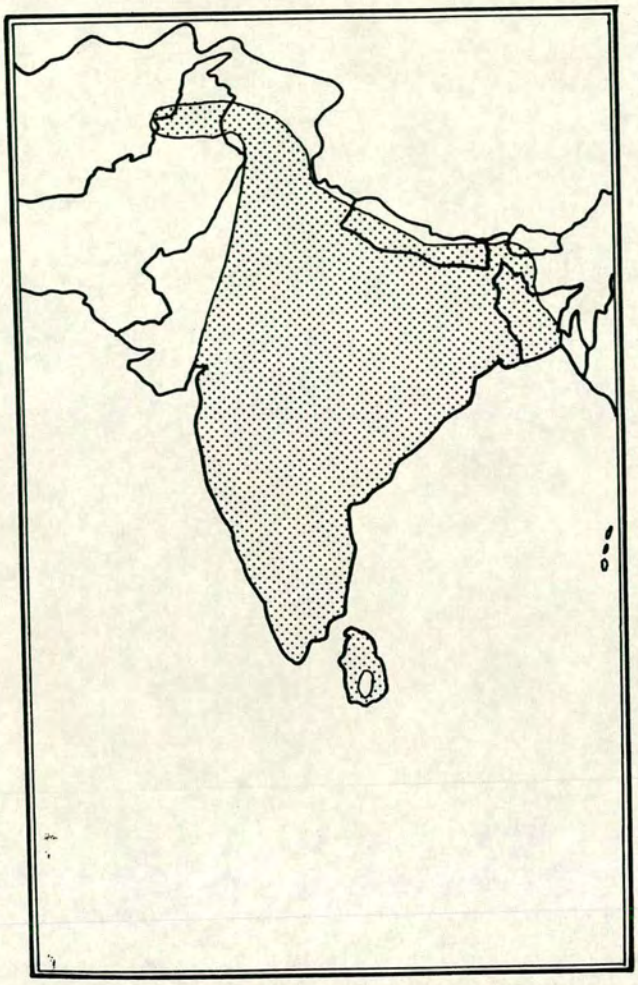


**Figure 1- 3 Distribution of the subgenus *Semnopithecus* (*Presbytis entellus*) (from Figure 3.16, Oates et al., 1994)**

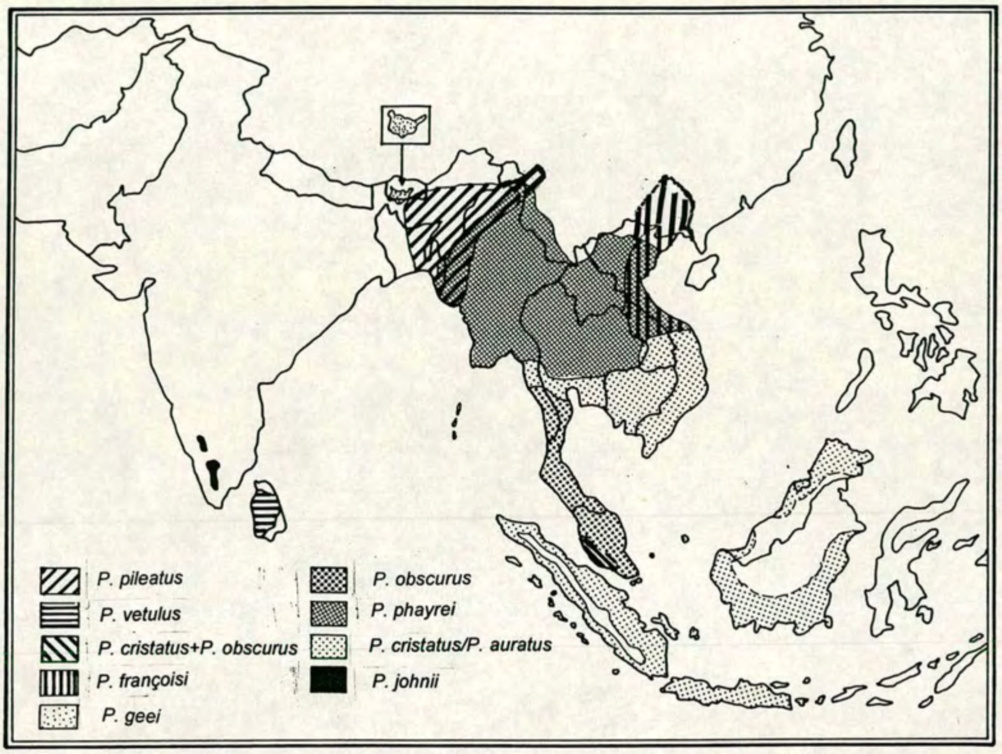


**Figure 1- 4 Distribution of the subgenus *Trachypithecus* (from Figure 3.12, Oates *et al.*, 1994, modified according to Li 1993)**

occurs in a small area in Bhutan and western Assam, and is replaced by a much larger distribution range of *P. (T.) pileatus* to the east of the Manas River, including a large part of Assam, the eastern part of Bangladesh, northwest and north Burma, and the northwest of Yunnan in China. These two species both dwell in Sal and other types of tall, moist deciduous forest under 100m a.s.l. (Mukherjee & Saha, 1974; Green, 1978; Mukherjee, 1978; Green, 1981). *P. pileatus* occurs in dense seasonal rainforest below 1500m a.s.l. in Yunnan (Ma, 1989).

In western Burma, the capped langurs are gradually replaced by Phayre's langurs (*P. (T.) phayrei*), whose distribution range overlaps in turn with that of François' langurs (*P. (T.) françoisi*) in Vietnam and Laos. Phayre's langurs occur in an area covering most of Burma (the east of Irrawaddy River), most of Laos and Thailand, from north to central Vietnam, and western and southern Yunnan, China. In China, Phayre's and François' langurs are allopatric (Li, 1993a); Phayre's langurs are to the west of Yuanjiang River (= Red River). This area is the eastern extension of the Himalayas. Langurs are found between 500 and 1600m a.s.l., but mainly below 700m a.s.l (Li & Lin, 1983). François' langurs (including white-headed langurs) are found on limestone hills to the east of the Yuanjiang River between 120 and 1400m a.s.l (Li, 1993a). Due to the difference in topography, forest types are also different between the two sides of the river (Wang *et al.*, 1989) (see *Plate 1- 2* for a comparison).

In south Thailand, Burma, Laos and Vietnam, Phayre's and François' langurs are replaced by the silvered langur (*P. (T.) cristatus*) whose distribution range covers southern parts of Vietnam, Laos, Burma, and Thailand, and Cambodia, the Malayan Peninsula, and Sundaland. In the northern part of their range, they live in inland, tall forests of Cambodia, Vietnam and southern Thailand (Lekagul & McNeely, 1977). Further south in the Malayan Peninsula and Sunda Islands, they are found only in riverine and coastal swamp forests (Medway, 1977; Marsh & Wilson, 1981; Payne *et al.*, 1985). The close relative of silvered langurs, *P. (T.) auratus*, occurs in Java where it is restricted to coastal and riverine habitats.

Dusky langurs (*P. (T.) obscurus*) are also distributed in the Malayan Peninsula, but live in the inland forests. They share the forest at Kuala Lompat with

**Plate 1- 2 Comparison of landscape and habitat between the south-eastern extension of the Himalayas (west of Yuanjiang River) and limestone hills (at east of Yuanjiang River)**

A. Himalayas topography; B. Karst (limestone) topography (photographed by the author) banded leaf-monkeys (*P. (P.) melalophos*). The forest here is extremely diverse; there are on average 159 species per hectare (Raemaekers *et al.*, 1980; Bennett,1983). Dusky langurs use predominantly the upper canopy of the forest, whereas banded leaf-monkeys use all levels.

(c) *The subgenus Presbytis* is restricted to rain forest in southern Thailand, the Malayan Peninsula, and the Sunda Islands (see *Figure 1- 5*). In addition to the Malayan Peninsula, banded leaf-monkeys are also found in most parts of Sumatra, the northwest of Borneo, and some small islands. At the north end of Sumatra are Thomas' leaf-monkeys (*P. (P.) thomasi*), which were studied in old rubber estates and fruit gardens (Gurmaya, 1986). Little is known about their ecology in primary forest.

Javan leaf-monkeys (*P. (P.) comata*) occur in western Java. They live in montane/submontane forest. At Kamajong, Java, their distribution can be as high as 1500m a.s.l. (Ruhiyat, 1983). Hose's leaf-monkeys (*P. (P.) hosei*) occur in northeastern Borneo. They live in evergreen forest between sea level and 150m a.s.l. At Sepilok, they shared the forest with maroon leaf-monkeys (*P. (P.) rubicunda*), but are rarer than maroon leaf-monkeys (Davies & Payne, 1982). However, at other sites, Hose's leaf-monkeys are more abundant than maroon leaf-monkeys (Rodman, 1978; Davies & Payne, 1982; Bennett, 1992). In addition to Sepilok to the northeast of Borneo, maroon leaf-monkeys are also found in other areas including central and eastern Borneo. At Tanjung Puting, they live in evergreen, mixed dipterocarp/heath, and peatswamp forest. White-fronted leaf-monkeys (*P. (P.) frontata*) occur in the north and southeast of Borneo. Little is known of the ecology of this species.

### 1.3.3 Distribution of the genus *Presbytis* in China

There are five *Presbytis* species in China: *P. (S.) entellus* (including two subspecies: *P. e. lania* and *P. e. schistaceus*), *P. (T.) pileatus*, *P. (T.) phayrei*, *P. (T.) françoisi*, and *P. (T.) leucocephalus*. Four of these species are at the northern limit of their distribution range. Only the white-headed langur (*P. leucocephalus*) is endemic to

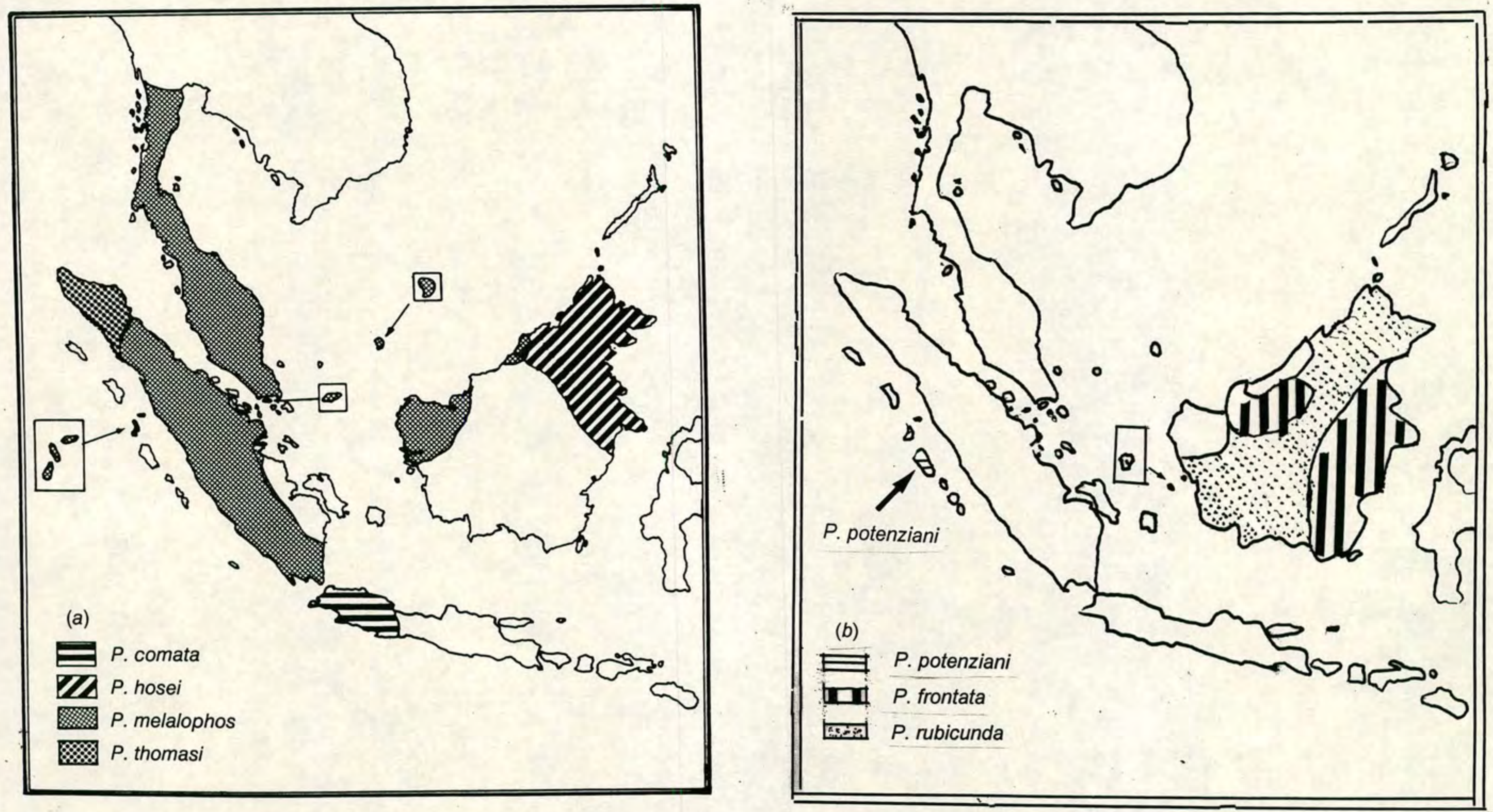


**Figure 1- 5 Distribution of the subgenus *Presbytis* (from Figure 3.11, Oates *et al.* 1994, modified according to Bennett & Davies 1994)**

China. Hanuman langurs (*P. entellus* ) are reported from 4 spots (see *Figure 1- 6*) in south Tibet, about 85 - 99°E and beside the line of 28°N. They occur mainly in riverine tropical seasonal rain forest, subtropical evergreen broad-leaf forest, and warm temperate mixed coniferous and broad-leaf forest under 2800m a.s.l. (Shen, 1963; Feng, 1986). No systematic study has been conducted on the ecology of Hanuman langurs in China.

Capped langurs (*P. pileatus*) occur only in a very small area (Dulongjiang of Gongshan County) in the northwest of Yunnan (see *Figure 1- 7*). They live in closed seasonal rain forest under 1500m a.s.l. on the north of Gaoligongshan Mountain that borders China and Burma (Ma, 1989). There is no systematic study on the ecology of this species. It was assumed that it might have gone extinct due to logging (S.L. Ma, *pers. comm.*), but it seems to be still living there (G. Hu, *pers. comm.*)

From the south of Gaoligonshan Mountain through southwestern to southern Yunnan (at the western side of Yuanjiang (Red) River), about 97.5 - 102°E and at the south to 25°N, several isolated populations of Phayre's langurs (*P. phayrei*) are found due to habitat fragmentation. They occur in tropical rain forest, seasonal rain forest, and subtropical evergreen broad-leaf forest between 500 and 1600m a.s.l. (Wuliangshan Mountain in Jingdong County), but mainly below 700m a.s.l. (He & Yang, 1982).

Across the Yuanjiang River, karst topography is distributed in a vast area from eastern Yunnan to Guizhou Province and Guangxi Zhuang Autonomous Region. A typical feature of this topography is the numerous limestone hills soaring above flat ground (*Plate 1- 2B*). François' langurs (*P. françoisi*) were reported from 23 counties in Guangxi and eight counties in Guizhou from the south of Guangxi through the southwest, the west and the northwest of Guangxi, to the southwest of Guizhou. Another population is found in the northeast of Guizhou (Wu, 1983; Wu *et al.*, 1987; Li & Ma, 1989; Shen, 1990). The whole distribution range is in an area of about 21.7 - 29.1°N and 104.8 - 108.8°E, ranging between 120 and 1400m a.s.l. Inside this range, white-headed langurs (*P. (T.) leucocephalus*) occur in four of the 23 counties in Guangxi. Their distribution range is surrounded by the Mingjiang River, the Zuojiang River, and the Shiwandashan Mountains, about 22°10' - 22°40'

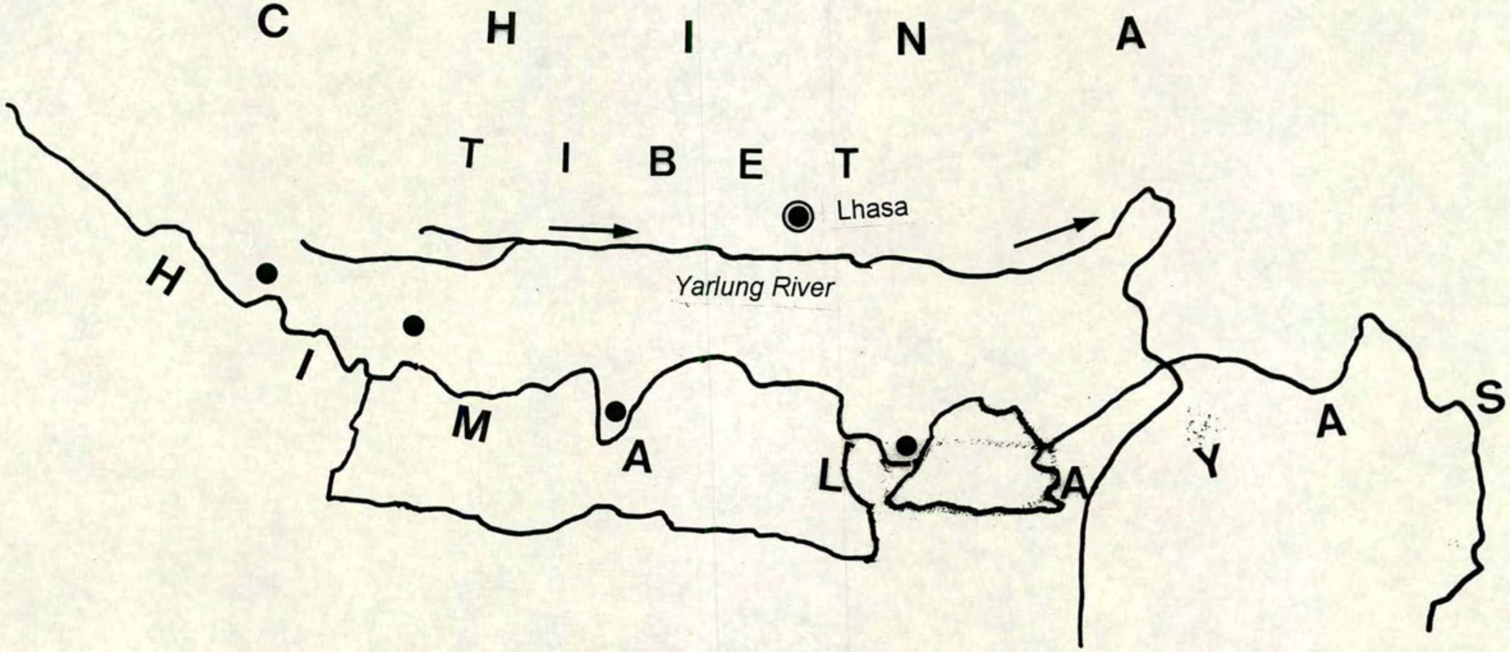


**Figure 1- 6 Distribution of Hanuman langurs (*Presbytis entellus*) in China (From Li, 1993)**

● known localities where Hanuman langurs occur

**Figure 1- 7 Distribution of *P. pileatus*, *P. phayrei*, *P. françoisi*, and *P. leucocephalus* in China**

▤ *P. pileatus* ▥ *P. phayrei* ▨ *P. françoisi* ▧ *P. leucocephalus*

N and 107° - 108° E. Limestone hills are in general low and white-headed langurs are found between 100 and 300m a.s.l. These two langur species are not sympatric; outside the surrounded area is the François' langur and inside is the white-headed langur. However, the two rivers did not seem to isolate these two langur forms in their evolutionary history (Lu & Li, 1991). The Shiwandashan Mountains did not seem to be an effective barrier either, because the highest peak is 1462m a.s.l. and the average height of the range is around 1000m a.s.l., lower than the upper limit of elevation of the distribution of François' langurs in the northwest of Guangxi (1400m a.s.l.) and in Guizhou (similarly 1400m a.s.l.). How these two langur forms kept separate in their evolutionary history is an interesting question and is closely related to their classification.

It is claimed that some hybrids of François' and white-headed langurs have been found in Luobai Reserve in Chongzuo County (Li & Ma, 1980). Limestone hills appear in clusters. Vegetation on the flat ground has been cleared and the land has been used for agricultural activity, human settlement, and highway construction (detailed in Chapter II). These activities have caused the habitat to be fragmented and these langur populations isolated, the history of which can be traced back at least 500 years ago, according to the county's annals. White-headed langurs in Luobai Reserve and Bapen Reserve are some 50km away from François' langurs. This distance prevents hybridisation. According to the original description, the hybrids had a white head and a black tail, which is similar to the coloration pattern of *P. f. poliocephalus*. In fact, there are white-headed individuals with different proportions of black fur on the tail in Bapen Reserve (*pers. obs.*), though white-headed and black-tailed individuals in general are rare. So these supposed hybrids may be only a variant coloration pattern.

A similar report is that Chinese zoologists have seen *leucocephalus* and *delacouri* living sympatrically without interbreeding (Ratajszczak, 1988; also see Oates *et al.*, 1994). However, according to an earlier survey in 1988, François' langurs are distributed at the southern side of the Mingjiang River in Ningming County (Longrui Reserve) (Li, 1993a); *i.e.*, it is in this area that the nominate subspecies *françoisi* is intermediate between *leucocephalus* and the Vietnamese subspecies of François' langurs.

## 1.4 Studies on the Socioecology of *Presbytis* species

### 1.4.1 Subgenus *Semnopithecus*

The Hanuman langur (*P. (S.) entellus*) was the first colobine monkey in Asia to be studied (McCann, 1928, 1933). It is an exceptionally adaptable species (Bennett & Davies, 1994), occurring in a variety of habitat types (see above) and showing a wide variation in physical features (Roonwal & Mohnot, 1977; Napier, 1985). This species does not occur in evergreen forest; instead, they seem to prefer open habitat. Hanuman langurs have been studied at more than 20 sites in India, Sri Lank, Nepal, and Bangladesh (Bennett & Davies, 1994), but much of the work is on social behaviour rather than ecology. This situation continued until recently (Bennett & Davies, 1994).

Hanuman langurs have a variable diet. At Kanha, mature leaves alone made up 35% of the diet and fruits only 24% (Newton, 1992). The langurs were found to feed on 53 species of trees and climbers and no single species predominated over the whole year. Near Simla, they fed mainly on cones of *Abies* and *Taxus* spp., along with their bark, cambium and twigs, and some herbs in the winter. Their diet was much more diverse in the summer; fruits and seeds, including acorns and pine-cones, made up the major part of the diet (Sugiyama, 1976). This diet seems to be an adaptation to alpine habitat where coniferous trees are abundant. In Polunnaruwa, mature leaves accounted for only 20% of the diet, whereas the proportion of fruits increased up to 45%. A total of 43 species were recorded as eaten (Hladik, 1977). Ten of these species accounted for 70% of the langur diet, and as at Kanha, no single species predominated over the whole year.

The social system is also variable. At Kanha, there are polygamous groups (each consisting of one adult male, about ten adult females and their offspring) and all male bands (consisting of subadult and adult males) (Newton, 1987). Both females and males migrated between bisexual groups, but the males did so much more frequently. Near Simla, group size varied markedly from 7 to about 100, but mainly between 12 and 47 (Bishop, 1979). All-male bands were rare in the montane environment; instead, males kept solitary or in some cases in pairs when outside a bisexual group (Boggess, 1979, 1980). In Ramnagar, South Nepal, Hanuman langurs live in multi-male and multi-female groups in which immature males appeared to prepare for leaving their natal group and immature females developed relationships with other group members (especially females) (Nikolei & Borries, 1997). Mating was seasonal, occurring from May to September. Outside this mating period, a bisexual group contained more than one adult male, but only one male could stay in the group during mating. Some of the males emigrated permanently and others temporarily. In Polunnaruwa, Hanuman langurs lived in groups ranging from 20 to 30 animals and containing more than one adult male throughout the year (Ripley, 1970). Group take-over is closely related to maintaining the social system. Its process was violent both in Kanha, where infanticide has been reported, and Polunnaruwa, and less violent near Simla (Ripley, 1967; Bishop, 1979; Newton, 1986).

Home range size varied according to habitat types. In peninsular India, the home range was 4 ha in villages and farms, 20ha in dry deciduous forest, 60 – 96ha at the edge between grassland and forest, and 390ha in moist deciduous forest (Oppenheimer, 1977; Newton, 1987). Himalayan Hanuman langurs have a larger home range. It increased with altitude from 20 ha in upper monsoon forest at 1200m a.s.l., 190ha in moist temperate forest at 2000m a.s.l., 210ha at the edge of temperate forest and meadow at 2800m a.s.l., and 760ha at the edge of temperate forest and meadow at 3000m a.s.l. (Vogel, 1971; Curtin, 1975; Sugiyama, 1976; Boggess, 1976; Bishop, 1979).

### 1.4.2 Subgenus *Trachypithecus*

Nilgiri langurs (*P. (T.) johnii*) have been studied in detail at four sites in the Western Ghats of southern India: Ootacamund (Poirier, 1968a, b, 1969a, b, 1970a, b), Periyar (Tanaka, 1965; Horwich, 1972), Kakachi (Oates, 1979; Oates *et al.*, 1980) and Mundanthurai (Hohmann, 1988, 1989a, b; Hohmann & Vogl, 1991), including three habitat types: evergreen Shola forest (Ootacamund and Kakachi), deciduous forest (Periyar), and gallery forest (Mundanthurai).

In the evergreen forest (Kakachi), Nilgiri langurs had 115 species of plants in their diet, of which only 3 tree species made up 45% of their diet. The two commonest species in the forest contributed only 5%. Leaves accounted for around 60% of the diet (young leaves > 30% and mature leaves < 30%). Fruits made up nearly 30%. Soil-eating and insectivory have been reported from this langur species. No data are available on their diet in the other two habitat types.

The social system of Nilgiri langurs is not so variable as Hanuman langurs. Nilgiri langurs normally live in polygamous groups (one adult male, several adult females, and their offspring) at all sites, averaged at 8.9 individuals in size in Ootacamund and 7.6 in Mundanthurai. Solitary males and predominantly-male bands were found in a small proportion of the population. Resident males were challenged and excluded by males from those bands and on one occasion the original polygamous group split into a new polygamous group and a multi-male group (Poirier, 1969a, b). An interesting phenomenon is the fission/fusion social system in this species (Hohmann, 1989). A stable subgroup was formed from the original group, having agonistic interactions with the dominant adult male and occupying part of the original group's home range. This may be related to another fact that subadult and juvenile animals were generally not excluded from their group after the male replacement. No infanticide was reported. This pattern has not been found in other langur species.

Home range size was smaller in deciduous forest, ranging from 5.6ha to 8.3ha in Periyar. It was much larger in the evergreen forest, ranging from 24ha in Kakachi to 240ha in Ootacamund. Home range size seemed to be influenced by langur group size, their ability to display, and the vegetation (Poirier, 1969b). Polygamous groups actively defended their home ranges, with little home range overlap (10% in Kakachi).

The close relative of Nilgiri langurs is the purple-faced langur, *P. (T.) vetulus*. This species is sympatric with Hanuman langurs in the semi-evergreen forests of central Sri Lanka. Purple-faced langurs had a diet different from that of Hanuman langurs, which resulted in their different patterns of range use and social behaviour (Bennett & Davies, 1994). Purple-faced langurs exploited a small number of common species and only 3 tree species accounted for 70% of their annual diet (Hladik, 1977). Only 28 species in total were found in their diet. While Hanuman langurs ate more fruits, purple-faced langurs were more folivorous, with leaves accounting for about 60% of their diet and fruits for only about 30%. Hanuman langurs in this area lived in large multi-male groups, whereas purple-faced langurs lived in small polygamous groups (averaged 8.4 individuals per group) which were maintained by group-takeovers (Rudran, 1973). Infanticide was assumed. Predominantly male bands contained only juvenile males and females that were reproductively inactive. Purple-faced langurs lived in tiny home ranges (2 to 3ha in size) that were defended fiercely, and all-male bands occupied ecologically sub-optimal habitats. Hanuman langurs lived in much larger home ranges (17 to 18ha). These differences may prevent competition between these two species.

Purple-faced langurs were similar to their close relative Nilgiri langurs in (1) leaves accounted for a larger proportion of their diet, (2) they lived in polygamous groups of similar group size, (3) there existed predominantly male bands, and (4) they actively defended their home ranges. They were different, because (1) purple-faced langurs did not feed selectively on diverse widely spread plant species, (2) a fission/fusion social system was not found in purple-faced langurs, and (3) infanticide was not found in Nilgiri langurs.

Hanuman langurs are replaced by Golden langurs (*P. (T.) geei*) and capped langurs (*P. (T.) pileatus*) in Assam (India) and Bhutan. The Assamese forests mark the area of this replacement. The latter two species further replace each other; golden langurs occur to the west of Manas River and capped langurs to the east. These two species were ecologically very similar. In addition to similar forest types, both species lived predominantly in polygamous groups (McCann, 1933; Mukherjee & Saha, 1974; Mukherjee, 1978; Gittins, 1980; Islam & Husain, 1982), with an average group size of 9.6 individuals/group, slightly larger than that in golden langurs and 7.5 - 8.3 in capped langurs. They appeared relaxed during inter-group interaction and their home ranges overlapped extensively (Mukherjee & Saha, 1974; Islam &

Husain, 1982; Stanford, 1991). The home range size of golden langurs (64ha) was larger than that of capped langurs (14-24ha, mean = 21.6ha).

Further data have not been reported for golden langurs. Stanford (1991) has studied capped langurs in detail in Madhupur, Bangladesh. There, only 35 plant species were found in capped langurs' diet. Mature leaves contributed a substantial portion (42%) of the diet. Young leaves accounted for a small portion (< 20%) and fruits made up less than 30%. The species-poor diet was closely related to the low plant species richness (c.f., only 28 tree species were recorded in a 1.2ha area, 5% of the study group's home range). Plant species richness was similarly low in Kanha (see above), but Hanuman langurs and capped langurs had different foraging strategies, which may be related to the annual rainfall (Bennett & Davies, 1994). Capped langurs were more arboreal, and they rarely moved on the ground. They saved energy by reducing their day ranges and playing less when mature leaves dominated their diet.

Phayre's langurs (*P. (T.) phayrei*) were different from capped langurs in several respects (Fooden, 1971; Green, 1978; Gittins, 1980; Zhang *et al.*, 1981; Farid Ahsan, 1984; Zheng, 1993). Phayre's langurs lived in evergreen forest rather than moist deciduous forest. They both lived in polygamous and multi-male groups, the size of which (3 – 30, mean 12.9 individuals/group) was larger than that of capped langurs (ranging from 5 to 13). The home range size was also larger (30ha in Phayre's vs. 14-24ha in capped). In southwestern Yunnan, China (Zheng, 1993), a species from the family Rosaceae accounted for 60.2% of the langurs' diet during a 20-day observation and young leaf of 4 plant species made up over 70% of the diet.

Little was known of the ecology of François' langurs (*P. (T.) françoisi*) and white-headed langurs (*P. (T.) leucocephalus*) before this study. About 27 plant species from 17 families were reported for the diet of François' langurs in Guangxi and over 30 species in Guizhou, China (Huang *et al.*, 1983; Li & Ma, 1989). White-headed langurs fed on 21 plant species from 14 families (Lai, 1987). These two langur species were reported to have similar plant species in their diet. They fed mainly on leaves and lived in polygamous groups (Huang *et al.*, 1983; Lai, 1987; Li & Ma, 1989; Yang & Hong, 1990; Li, 1993a). Solitaries have been found in white-headed langurs. White-headed langur groups ranged from 3 to 18 individuals/group in size, averaged 7.7 (Li, 1993a). All these reports have provided a basis for further intensive study on their ecology, but none of them has studied their basic ecological requirements in detail. An important question has not been answered; *i.e.*, whether limestone hills are the preferred habitat of these langurs or their last refuge, a question which will be tackled in Chapter V.

Silvered langurs (*P. (T.) cristatus*) and lutungs (*P. (T.) auratus*) are close relatives. The former species occurs in a large area, but the latter is restricted to Java. Due to the difficulties of following animals in mangroves, these two species were studied mainly in their fringe habitat: Kuala Selangor in Peninsular Malaysia and Pangandaran in western Java (Bernstein, 1968; Wolf & Fleagle, 1977; Wolf, 1980; Kool, 1989). Habitat types include evergreen forest, parkland, and mangrove/teak plantation. Leaves (mostly young leaves) accounted for 55% of the lutungs' diet (Kool, 1989) in Pangandaran. Both species lived predominantly in polygamous groups. The group size of silvered langurs ranged between 9 and 30 individuals/group in evergreen forest in Kanchamburi (Thailand), 11 and 38 in the parkland in Kuala Selangor. That of lutungs in Pangandaran ranged between 6 and 23. Solitary males and all-male bands were reported (Wolf & Fleagle, 1977). Violent group takeovers and infanticide also existed in silvered langurs. Home range size of lutungs was between 2.5ha and 8ha in Pangandaran. Silvered langurs did not show territoriality, but lutungs did.

Dusky langurs (*P. (T.) obscurus*) occur extensively in the rainforest of South-east Asia. Kuala Lompat in the centre of Peninsular Malaysia is the site of intensive primate studies since the late 1960's (Chivers, 1980). This site is different from other sites, because dipterocarps only comprised 4-16% of the total tree basal area and leguminous trees comprised 11-26% (Bennett, 1983), which provided rich food sources for colobine monkeys (Waterman *et al.*, 1988). In other sites, dipterocarp trees dominated the forest and provided little food for colobines (Medway, 1972; Chivers, 1974; Marsh & Wilson, 1981; Whitmore, 1984; Davies *et al.*, 1988), due to the relatively low ratio of protein to fibre and the high proportion of terpenes in their leaves (Waterman *et al.*, 1988). The forest at Kuala Lompat is also extremely diverse (see above) with an average of 159 tree species per hectare (Raemaekers *et al.*, 1980; Bennett, 1983).

Dusky langurs fed mainly in the upper canopy where legumes and other colobine food tree families were abundant (Curtin, 1980; MacKinnon & MacKinnon, 1980). Leaves made up 47% of their diet (young leaves accounting for 36%) and fruits about 35% (Curtin, 1980). They also ate seeds (accounting for about 10%). They generally lived in polygamous groups. Solitary males and all-male bands, or predominantly male bands, have not yet been reported. Langur groups had a home range of about 33ha in size that was defended.

### 1.4.3 Subgenus *Presbytis*

At Kuala Lompat, another colobine monkey species, the banded leaf-monkey (*P. (P.) melalophos*), was studied in comparison with dusky langurs. While dusky langurs obtained food mainly from the upper canopy, banded leaf-monkeys fed at all levels of the forest (Curtin, 1980; MacKinnon & MacKinnon, 1980). It is thus not surprising that banded leaf-moneys had a more diverse diet than dusky langurs. Banded leaf-monkeys were more frugivorous, with 46% of the diet comprising fruits and seeds and 17% flowers. Mature leaves made up nearly 30% of the diet. About 9.6% (5 species) of the trees in the forest made up 45% of the diet (Bennett, 1983, 1986). Such dietary niche separation prevented competition between these two species and allowed them to coexist in the same forest.

The favourite fruits, seeds, and flowers of banded leaf-monkeys were in general from large common trees at Kuala Lompat. However, in the primary forest in Sungai Tekam area in Peninsular Malaysia, food trees were on average smaller in size, but more common in number than those at Kuala Lompat (Bennett, 1986). These species synchronised leafing, flowering and fruiting, so food supply was only available from any one species for a short time. At Kuala Lompat, the rarity of large food trees reduced the advantage of defending food sources, because food supply was curtailed by trees that no longer produced preferred foods, but not by other animals eating them. In Sungai Tekam, however, the cost of allowing other groups to feed in a small tree was great, but the number of these trees indicated that a group could obtain all of its food from a relatively small area. As a result, banded leaf-monkeys appeared more territorial in Sungai Tekam than at Kuala Lompat (Bennett, 1986). Breeding males kept spacing between groups by regularly vocalising at night. Home range in Sungai Tekam (14.5ha) was smaller than at Kuala Lompat (29.5ha) (Bennett, 1986; Johns, 1986).

Banded leaf-monkeys at both sites lived in polygamous groups, containing about 15 individuals. Males migrated between groups. Young males either kept solitary or joined an all-male band. In Sungai Tekam, an all-male band was confined to an area of food-poor forest (Johns, 1983), as was the situation in purple-faced langurs (see above).

The soils of inland Borneo are generally very poor and low in nutrients (Davies & Baillie, 1988). Abundant dipterocarps in the forest provide little food for colobines, despite the high plant species richness of the forest (Waterman *et al.*, 1988). The mature leaves of the ironwood, *Eusideroxylon zwageri* (Lauraceae), the only common large non-dipterocarp tree, were very indigestible (Davies, 1984). Such habitat was severe for colobines. Only one species (the silvered langur) occurs in Borneo but is restricted to mangrove, peat swamp and riverine forest of the coastal plain which provide higher primary productivity. In inland forest, maroon leaf-monkeys (*P. (P.) runbicunda*) at Sepilok lived on the rarest trees in the forest. The common dipterocarps and species from the family Lauraceae made up only 3.6% of their diet. Because of the scarcity of palatable trees, lianas contributed 32% to the monkeys' annual diet (Davies, 1991). These monkeys preferred young leaves (accounting for nearly 40%) and seeds (about 30%). As in banded leaf-monkeys, they increased food plant species diversity when their preferred foods became scarce. The difference from banded leaf-monkeys was that maroon leaf-monkeys ate few mature leaves (1%) at any time of the year (Davies *et al.*, 1988).

Maroon leaf-monkeys lived in polygamous groups, ranging from 3 to 9 animals in size. Subadult males formed all-male bands. Both males and females migrated between groups (Supriatna *et al.*, 1986). Violent fighting was involved in group takeovers (Davies, 1987). Because the monkeys ate foods that were widely distributed, they had large home ranges (mean = 84ha) and vigorously defended their ranges (Davies, 1984).

The socioecology of other species of this subgenus, including *P. comata* (Javan leaf-monkeys), *P. frantata* (white-fronted leaf-monkeys), *P. potenziani* (Mentawai leaf-monkeys), *P. hosei* (Hose's leaf-monkeys), and *P. thomasi* (Thomas' leaf-monkeys), is much less known. Hose's leaf-monkeys are sympatric with and rarer than maroon leaf-monkeys at Sepilok (Davies & Payne, 1982). At other sites in Borneo, Hose's leaf-monkeys are more abundant (Rodman, 1978; Davies & Payne, 1982; Bennett, 1992). It is not known how they avoid direct competition because they appear to have similar anatomy, diet and social organisation (Davies, 1994).

Habitat at Paitan on Siberut is similar to Sepilok. The forest is dominated by dipterocarps (accounting for 21% of tree species on this island) (Whitten, 1982). Legumes comprised 2.4% of stems (Davies, 1984; Waterman *et al.*, 1988). The endemic species on this island, the Mentawai leaf-monkey, lived in monogamous groups, consisting of an adult male, an adult female, and their offspring. It is interesting that another colobine species, *Simias concolor*, lived in a similar social system in the south of the island (Tilson & Tenaza, 1976; Tilson, 1977; Watanabe, 1981). The mated pairs of Mentawai leaf-monkeys duet in the same way as gibbons do (Tilson & Tenaza, 1976).

Fruit and seeds made up 61-66% and leaf matter 36% of the diet of Thomas' leaf-monkeys at Bohorok, Sumatra (Gurmaya, 1986), which was similar to the diet of banded leaf-monkeys at Kuala Lompat. Leaves accounted for 68% of the diet of Javan leaf-monkeys (young leaves = 62% and mature = 6%) (Ruhiyat, 1983), which was similar to the diet of the subgenus *Trachypithecus*. Javan leaf-monkeys lived in monogamous groups at Patenggang in west Java. Bennett & Davies (1994) believed that there was an underlying similarity between all species in this subgenus and the differences in socioecology were caused by differences in habitat.

Geophagy has been reported from several colobine monkeys, including *Colobus satanas* (Harrison, 1986), *C. badius* (Struhsaker, 1975; Struhsaker *et al.*, 1997), *C. guereza* (Oates, 1978), *Presbytis rubicunda* (Davies & Baillie, 1988), *P. melalophos* (Bennett, 1983), *P. johnii* (Oates *et al.*, 1980), *P. entellus* (Ripley, 1970;

Hladik, 1977), *P. vetulus* (Hladik, 1977), and other primate species (see Struhsaker *et al.*, 1997). This behaviour included soil eating, charcoal consumption, and selecting pond plants with high sodium concentrations. Reasons for this behaviour are poorly known. Early explanations suggested it functioned to regulate the pH of the fore-stomach (Poirier, 1970). Later, Hladik & Guegen (1974, cited in Kay & Davies, 1994) proposed physicochemical functions, suggesting that it was related to taste and absorption of toxins. A similar explanation is that charcoal functions to promote digestion by absorbing phenolics in food (Struhsaker *et al.*, 1997). It is also proposed that geophagy is related to mineral acquisition (Oates, 1978; Davies & Baillie, 1988).

### 1.4.4 Summary

*Presbytis* species can be divided into three ecological types: continental, peninsular, and island. According to data from 11 species, those of continental type (*P. johnii, P. geei, P. pileatus*, and *P. phayrei*) are generally more folivorous, with leaves accounting for over 60% of their diet. Species of peninsular type (*P. auratus, P. melalophos,* and *P. obscurus*) are less folivorous (leaves accounting for from 30% to 55% of their diet). Species of island type are most frugivorous (leaves accounting for 36 – 40% of the diet of *P. thomasi* and *P. rubicunda*, and fruits accounting for as high as 61 – 66% in *P. thomasi*). Exceptions are *P. vetulus* and *P. comata* (island type species with leaves accounting for respectively 60% and 68% of the diet), and *P. entellus* whose diet is so variable, with the portion of leaves in the diet ranging from 20% to 50%.

Comparisons between subgenera show that *Trachypithecus* species have a more folivorous diet, with leaves accounting for over 55% of their diet, and *Presbytis* species have a more frugivorous diet, with leaves accounting for less then 50% and fruits and seeds for over 40%. Exceptions are *P. obscurus* (a species of the subgenus *Trachypithecus* with leaves accounting for only 47% of the diet) and *P. comata* (a species of the subgenus *Presbytis* with leaves accounting for 68%, indicating that fruits account for only about 30%). The subgenus *Semnopithecus* (*P. entellus*) is intermediate between these two subgenera.

In social organisation, polygamous groups are the main social system, based on data from 14 species of the genus *Presbytis*. The occurrence of multi-male groups is rare in *P. johnii, P. phayrei*, and *P. entellus*, and does not correspond to their taxonomic relationship or ecotypes. It is interesting that *P. potenziani* lives in monogamous groups. Explanations for this exception have not been available. A sympatric colobine species, *Simias concolor*, has the same social system in the south of Siberut Island; but in the north, this species lives in polygamous groups, which is attributed to an anthropogenic change from primary to secondary forest or hunting pressure in the north (Bennett & Davies, 1994).

Differences in other aspects of socioecology, including group size, solitaries, all-male bands or predominantly male bands, and home range size, are not constant according either to taxonomic relationship or to ecological types. All these seem to be more sensitive to habitat changes.

## 1.5 Conservation Issues

### 1.5.1 Population declines

Shifting continents have changed climatic patterns (temperature and rainfall) since the Pleistocene. Recent Pleistocene glaciations and interglaciations led tropical forests to contract and expand, which repeatedly created and eliminated ecological niches for primates. These geo-historical events can be used to explain long-term changes of primate populations. However, the drastic decline in primate populations in the last century is attributed to the devastating effects of exploding human populations and economic development (Strier, 2000). Wild populations of nonhuman primates are in trouble in many of the 92 countries where they occur (Mittermeier, cited in Tuttle, 1998), especially in those nations richest in primates, *e.g*., Brazil, Perú, Colombia, Madagascar, Indonesia, China, and Vietnam (Wallis, 1997). Indeed, nearly 60% of nonhuman primate species are listed as rare, vulnerable, threatened, or endangered (Rowe, 1996). The endangered primate species list will become longer and longer if human activities do not undergo dramatic changes (Strier, 2000). For example, the population of Tana River red colobus monkeys (*Colobus badius rufomitratus*) declined by 80% between 1975 and 1985 due to a changing river course and shifting agricultural practice (Decker, 1994). Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) and Guizhou snub-nosed monkeys (*R. brelichi*) have declined in numbers to only about 2000 and 800 animals respectively (Schaller, 1985; Tan, 1985; MacKinnon, 1986) due to habitat loss and fragmentation, hunting and trapping (Zhao, 1988). François' langurs (*Presbytis françoisi*) and white-headed langurs (*Presbytis leucocephalus*) had constantly declined to 4000 - 5000 and 400 individuals respectively in China by the early 1980s due to hunting (Li & Sun, 1982; Wu, 1983). Gibbon populations (*Hylobates leucogenys/gabriellae*) in Laos have disappeared from smaller tracts of forest and several selectively logged and other degraded areas (Ruggeri & Timmins, 1996). The populations of rhesus macaques (*Macaca mulatta*) have declined due to commercial harvest and have not yet recovered and may never recover without direct intervention (Strier, 2000). Primates are threatened globally and there seems no single solution applicable to all endangered primates due to extinction risks varying greatly with the biology of each species and different natural or human-imposed disturbances.

### 1.5.2 Hunting

Hunting pressures on primates vary by region and affect primate species to different degrees. Orangutans, for example, are not eaten by indigenous people because they look like human beings (Galdikas, 1995). In other parts of the world, however, primates, from chimpanzees to spider monkeys, are hunted for their meat, skins, or medicinal use (Mittermeier, 1987). Folivorous primates are especially preferred by hunters for their meat due to their larger body size (Oates, 1996). In the Brazilian Amazon, a single family killed about 500 large primates in less than two years (Peres, 1990). In Surinam, about 25% of the available meat at local markets came from primates (Mittermeier & Cheney, 1987). In south-west Guangxi, China, medicinal wine made from François' langurs and white-headed langurs was an important economic income source in the 1970s (*unpubl. data*). Logging operations increase hunting pressures in two ways: one is to increase meat demand from the workers hired for logging operations, the other is to make remote forests more accessible to hunters seeking meat by vehicles to sell in local markets (Johns & Skorupa, 1987; Bennett, 1991; Wilkie *et al.*, 1992; Oates, 1996).

A recent trend in southwestern Guangxi is worrying. François' langurs have disappeared in some areas due to poor conservation management. Encheng Reserve in Daxin County, for example, was an important area for the protection of this species (Y.M. Lai, *pers. comm.*), and some early ecological observation was carried out on François' langurs in this reserve. However, no langurs have been found during a recent survey (Li, *unpubl. data*) and hunting is the main reason for the langurs' extinction in this reserve. In Bapen Reserve, hunting disappeared completely during 1988 and 1989, but became common in the 1990s. The incentive to launch this study on white-headed langurs was more or less the outcome of hunting that had pushed the langur population to the edge of extinction.

### 1.5.3 Habitat loss

Despite widespread concern about the effects of deforestation on global climate patterns and international treaties designed to prevent it, clear-cutting and burning continue to destroy significant areas of the world's remaining tropical forests (Strier, 2000). In addition to hunting, habitat loss is another important factor threatening primate populations, and its effects are more profound. More than 90% of all primate species occur in the tropical forests of Asia, Africa, Central and South America (Mittermeier, 1986). As these forests disappear, so too do the species living in them. Habitat loss has caused Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) to be restricted to a few forest patches (Zhao, 1988), and 70% of the original habitat of Vietnam snub-nosed monkeys (*R. avunculus*) has been lost (MacKinnon, 1986). In southern China, there is a vast area of limestone hills which is within the limits of the distribution of François' langurs in terms of coordinates, altitude, and climates. However, François' langurs are not found in this area. Much habitat of white-headed langurs is being lost to agricultural use even in protected areas (detailed in Chapter II).

### 1.5.4 Habitat fragmentation

Habitat fragmentation is a conservation issue that is closely related to habitat loss. When a vegetation belt is cleared through a forest, the clearance will result in other effects on the primates living in the remaining forest patches in addition to the absolute habitat loss. The area near the forest edge newly created by the clearance will receive more sunlight, so that the humidity will be lower and the temperature will be higher. Rare plant species originally living inside the forest will disappear. Thus the habitat in edge areas will no longer be available to primates living on these plants (Lovejoy *et al*., 1986). These edge effects result in relative habitat loss, because when the forest fragments are small enough, their plant species composition will be changed completely and these fragments will not be suitable to primates. Further absolute habitat loss will be caused.

Habitat fragmentation is also a global issue in primate conservation (Wilcover *et al.*, 1986; Rylands & Keuroghlian, 1988; Ferrari & Diego, 1995; Tutin *et al.*, 1997; Tutin, 1999). In China, Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*), François' langurs (*Presbytis françoisi*), white-headed langurs (*P. leucocephalus*), and Phayre's langurs (*P. phayrei*) are all living in fragmented habitats (see *Figure 1- 2*, *Figure 1- 6*, *Figure 1- 7*). In Vietnam, less than 300 individuals of the Vietnam snub-nosed monkey (*R. avunculus*) survive in four widely isolated forest fragments (Williams, 1992; Wirth, 1992), and, indeed, habitat fragmentation is a major threat to all primates in Vietnam (Nisbett & Ciochon, 1993). Because of their different biological nature, primate species respond differently to this problem (Rylands & Keuroghlian, 1988; Tutin, 1999). In Amazonian rainforest, *Pithecia pithecia* occurred in the fragment that was structurally most complex, with highest plant species richness; whereas *Saguinus midas* and *Alouatta seniculus* occurred also in other forest fragments that were less structurally complex, with lower species richness (Schwarzkopf & Rylands, 1989). This indicates that *P. pithecia* could tolerate the least habitat change. Because of heavy human population pressure, absolute wildlife conservation is often impossible. Efforts should be made to find a balance where humans and non-human primates can coexist. To reach this objective, the effects of habitat fragmentation should be studied species by species, so as to figure out conservation recommendations specifically applicable to local areas.

### 1.5.5 Habitat degradation

Habitat disturbance (*e.g.*, selective logging, firewood cutting, and herb collection) sometimes does not cause any obvious effects that are easily monitored. In the long term, however, this may cause habitat degradation, which in turn will change the behaviour and socioecological parameters of primate societies (Johns, 1983; Johns, 1985; Johns & Skorupa, 1987; Dunbar, 1987; Decker, 1994; Fimbel, 1994; Hill *et al.*, 1994; Johns & Johns, 1995; Oates, 1996; Menard & Vallet, 1997; Ganzhorn & Schmid, 1998; Rosenbaum *et al.*, 1998; Sterck, 1999). For example, the population of Tana River red colobus (*Colobus badius*) declined dramatically between 1975 and 1986 due to habitat disturbance (Decker, 1994). Before the disturbance, range size was smaller, range overlap occurred, and a greater portion of the forest was used per day and per month. Compared to the diet in 1986-1988, red colobus monkeys ate more leaves. Social behaviour can also be affected by habitat degradation. For example, Hanuman langurs (*Presbytis entellus*) played significantly less in degraded habitat than in habitat of high quality (Sommer & Mendoza-Granados, 1995). *Macaca fuscata yakui* in Yakushima were more easily seen in areas where logging was less recent and/or less extensive (Hill *et al.*, 1994). Pig-tailed langurs (*Simias concolor*) lived in polygamous groups in the north of Siberut and monogamous groups in the south (Watanabe, 1981), which was likely related to a change from primary to secondary forest in the north (Bennett & Davies, 1994). All these changes may be potentially profound to the survival of primates, thus the effects of habitat quality will be discussed in the present study on white-headed langurs (Chapter V).

## 1.6 Study Objectives

In white-headed langurs, two topics are interesting and deserve special emphasis. One is their classification and the other is their conservation. As has been shown above, the classification of white-headed langurs and François' langurs is still in dispute. Data on morphology and genetics suggest that they are two subspecies, whereas their distribution pattern does not support this. Because François' langurs are distributed over a much larger range than white-headed langurs, a promising approach is to compare the socioecology of these two forms, so as to explore differences in their basic ecological requirements. However, little is known about the socioecology of François' langurs. The present study on white-headed langurs will provide data for a comparison that will be completed in the near future.

White-headed langurs are vulnerable to further habitat loss. To safeguard the survival of these langurs in the wild, the effects of habitat fragmentation and habitat degradation need to be quantified. It is also important to document the current population size and its change over time. An objective of this thesis was to use this information as a basis of conservation recommendations. To reach this objective, the following questions will be answered in this research:

(a) How large is the current population size of white-headed langurs?
(b) How did the population size change over the past years?
(c) Which area of Bapen Reserve is preferred habitat?
(d) How does the food availability change throughout the year?
(e) How do langur groups compete for natural resources?
(f) How do other environmental factors influence white-headed langurs?
(g) How does habitat degradation influence the survival of white-headed langurs?
(h) And finally, how to effectively conserve the langurs in Bapen Reserve?

Chapter II

# THE STUDY AREA

## 2.1 Introduction

### 2.1.1 Climate

China crosses several climatic zones from the north tropics in the south to the cold temperate in the north (*Figure 2- 1*). Himalayan tectonic movement resulted in a general trend of elevation increasing from the east to the west, and complicated classification of climate zones. Two main regions are identified: a monsoon region in the east where topography is in general flat, and a montane region in the west where large mountains function to block the cold air current from the north in the winter. Because of the relatively flat topography, the cold current from Siberia in the winter reaches to the extreme south of the eastern monsoon region. According to information collected in Fusui County (A in Figure 2-1) between 1951-1980, the air temperature could be as low as -6.6 °C in the winter (January) though the area is in the tropics. In the summer, however, it was as high as 39 °C. Such a climatic pattern has made an important contribution to shaping a unique plant community with rich biodiversity in the area.

### 2.1.2 Vegetation

Guangxi Province is in the eastern monsoon region. It is one of the few provinces where plant species composition is most complicated in China (Guangxi Provincial Forestry Department, 1993). According to 1990 data, 25.34% of the land area in the province was covered by forest. There were over 8000 species of vascular plants belonging to 1700 genera from 284 families. In terms of floristic components, the vegetation is divided into flora of Indo-china, South China Sea, Yunnan, Burma, and Thailand in the south of the province; flora of East and Central China in the north; flora of South China in the east; and flora of Yunnan, Guizhou, and Guangxi in the west.

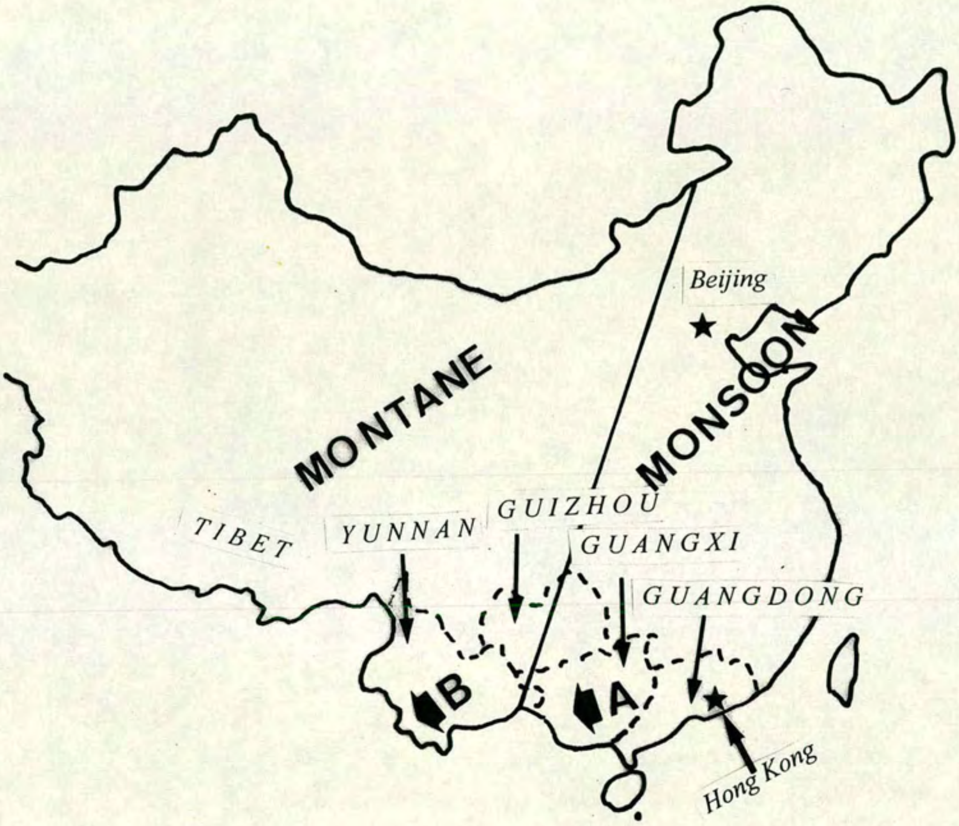


**Figure 2- 1 Two main climatic regions in China: a monsoon region in the east and a montane region in the west. A: the working area including the main study site, B: Xishuangbanna in Yunnan Province**

Because of the climatic pattern, many endemic species are found in South Guangxi (e.g., *Camellia nitidissima, C. longgangensis, Cathaya argyrophylla, Cyathea spinulosa*, and *Parashorea chinensis*). Compared to Xishuangbanna (B in Figure 2-1) that is at the same latitude in Yunnan, a province to the west of Guangxi, the floral composition in southwest Guangxi is more complicated (Wang *et al.*, 1989). The flora of tropical limestone in some areas is extremely rich. Chin (1977) lists 1216 species of angiosperms from limestone hills in Malaya, of which 261 (21.4%) are endemic to the Peninsula; 335 species are characteristic of limestone and 254 (20.8%) confined to it. Anderson (1965) estimated that there are over 600 species on the limestone hills of Sarawak. However, little is known in general about the species composition of limestone forests in China (Richards, 1996). In this chapter, data will be presented on the vegetation of limestone forest in Bapen Reserve, Southwest Guangxi, where the white-headed langur occurs.

### 2.1.3 Distribution of white-headed langurs

White-headed langurs are endemic to Southwest Guangxi, including parts of four counties (Fusui, Chongzuo, Ningming, and Longzhou) that are surrounded by the Mingjiang River, the Zuojiang River, and Shiwandashan Mountains (Chapter I and *Figure 2- 2*). Because of habitat fragmentation, the subpopulations of white-headed langurs are conserved in three reserves: Bapen (Fusui County), Luobai (Chongzuo County), and Longgang (Ningming and Longzhou Counties). The present study involves Bapen and Longgang Reserves, so there follows a general description of these two reserves. **The working area** included the whole Bapen and Longgang Reserves, but **the main study area** was located in a hill-group which contained the main population pool of white-headed langurs in Bapen Reserve (detailed in Chapter III).

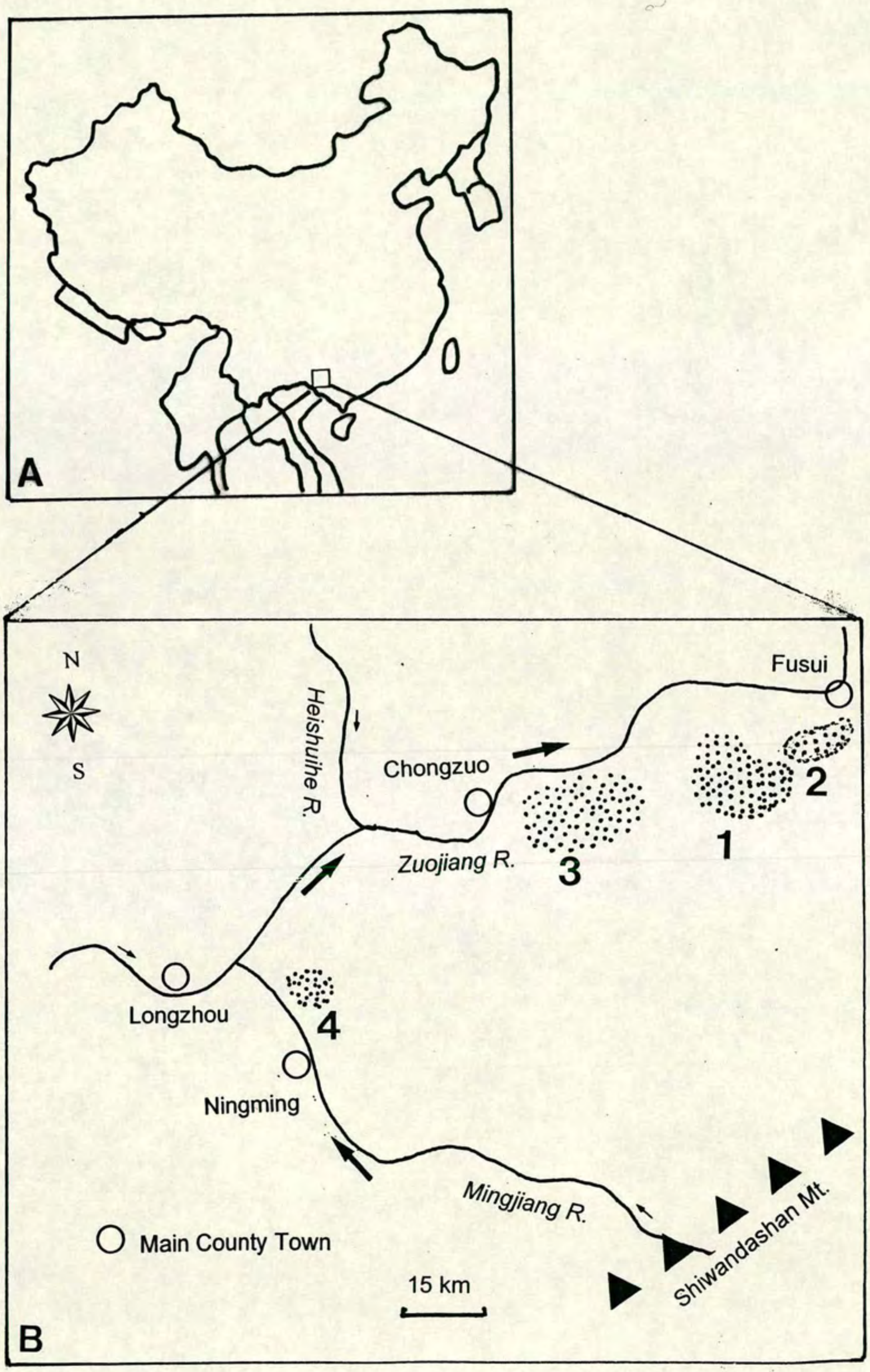


**Figure 2- 2 Distribution of world sub-populations of *P. leucocephalus***

A: Map of China showing the area of occurrence of the white-headed langur

B: Distribution of world sub-populations of white-headed langurs. Each patch represents a complex of limestone hills (Patches 1 & 2, Patch 1 includes hill-group MZ in Bapen Reserve, Patch 2 includes LGS, QN, & GP, GF is not included; 3, Luobai Reserve; 4, Longgang Reserve)

### 2.1.4 Working area: habitat fragmentation

Bapen Reserve is located at the north edge of the tropical zone, about 107°46'-108°03' E and 22°25'-22°31' N, with karst topography ranging from 110 to 359m above sea level (a.s.l.). The flat ground is cultivated by the local community (*Plate 2-1*). Stony hills are left to the Reserve for conserving wildlife including white-headed langurs. Hills occur in groups, which provide habitat for langurs. Because of cultivation surrounding the hill-groups, the habitat has been fragmented. The distance between the habitat fragments varies from 100 to 2,000m. In addition to cultivation, the flat ground has also been used for making roads and human settlements.

Hill-groups that were surveyed included Longgengshuang (LGS, 35.1km²), Qunan (QN, 12km²), Gengfeng (GF, 6km²), Gupiao (GP, 10km²), and Mozun (MZ, 34.3km²) (see *Figure 2- 3*). The border between LGS and GF was a river on which there was a dam. The river was about 50 m wide, but the distance from LGS to GF was about 100m. The dam was the only channel for individual exchange between langurs in these two hill-groups. Division between LGS and QN was arbitrary, because there was no definite natural demarcation between them. They were divided according to different topographic features. Mean height of hills in LGS was about 203m (n=15), and they were largely interconnected with each other; whereas the mean height in QN was only 165 m (n=15) and the hills were mostly discontinuous. The boundary between LGS and GP was a clear belt, the minimum width of which was about 1,000m. This belt was grassland before 1992 but has been cultivated since then. The distance from MZ to LGS was about 1,500m and to GP was about 2,000m. There were roads and six villages between these hill-groups. Though there was a small hill among them, it has been quarried for rock material for at least 20 years and there was no vegetation on the hill, so it did not function as a stepping stone for langur dispersal. It is clear that the habitat has been severely fragmented. The extent of fragmentation depended on the size of hills. Habitat fragments in QN were the smallest in size, but were much larger in LGS.

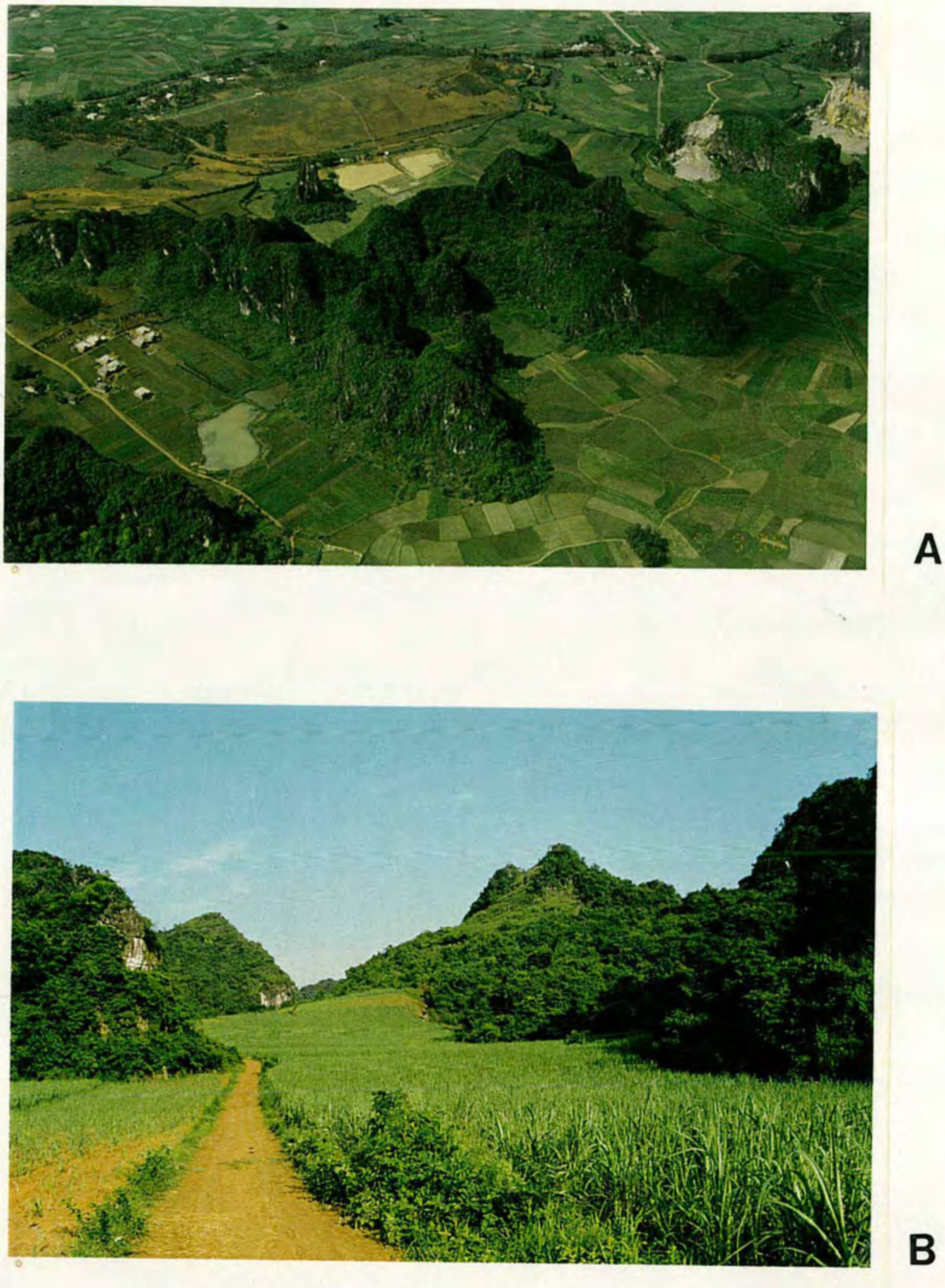


**Plate 2- 1 Habitat fragmentation due to the flat ground lost to agricultural use**

A. Aerial view of north-eastern end of the hill-group MZ;

B. B. Crops surrounding the habitat of limestone hills in the main study area.

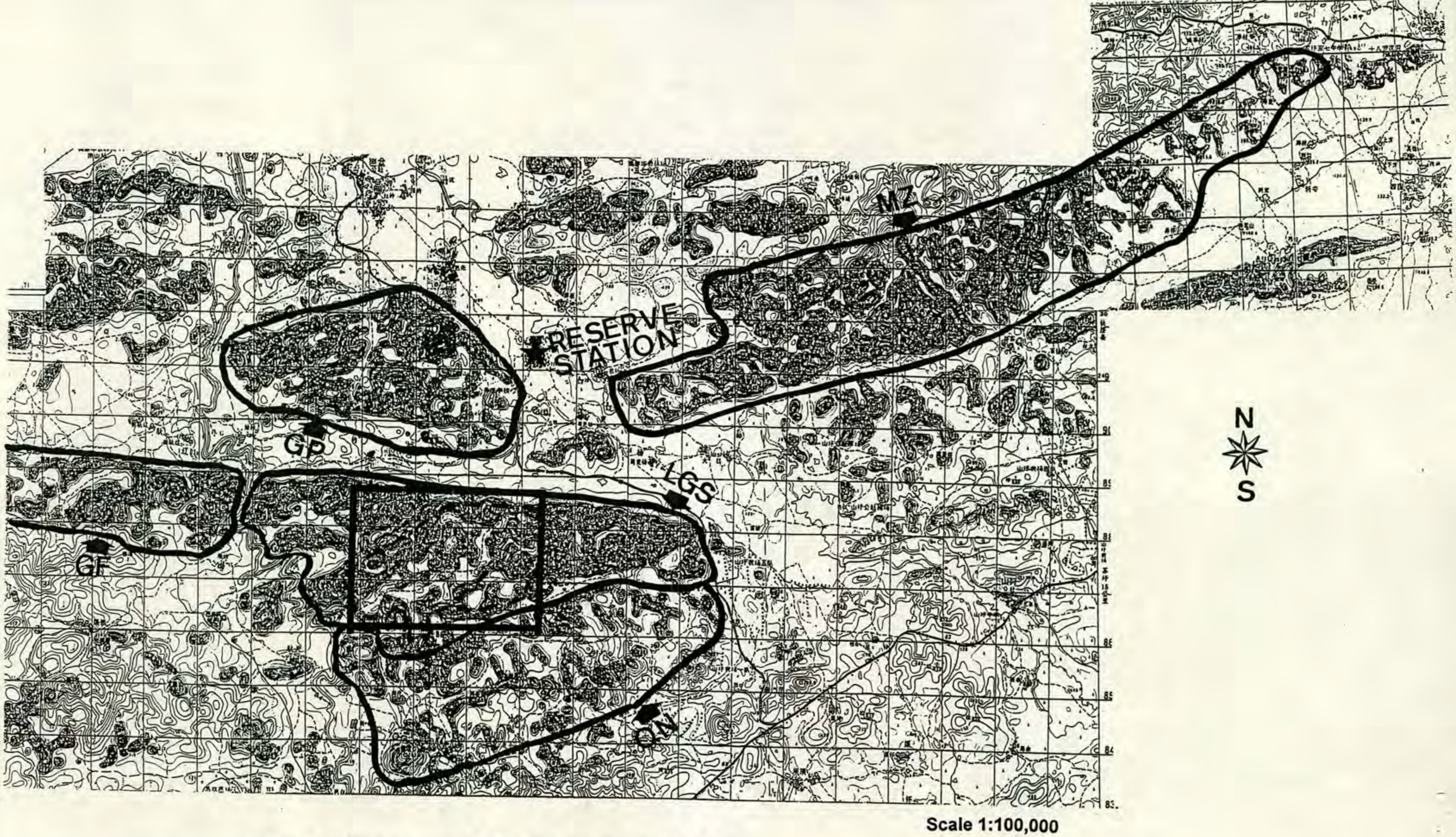


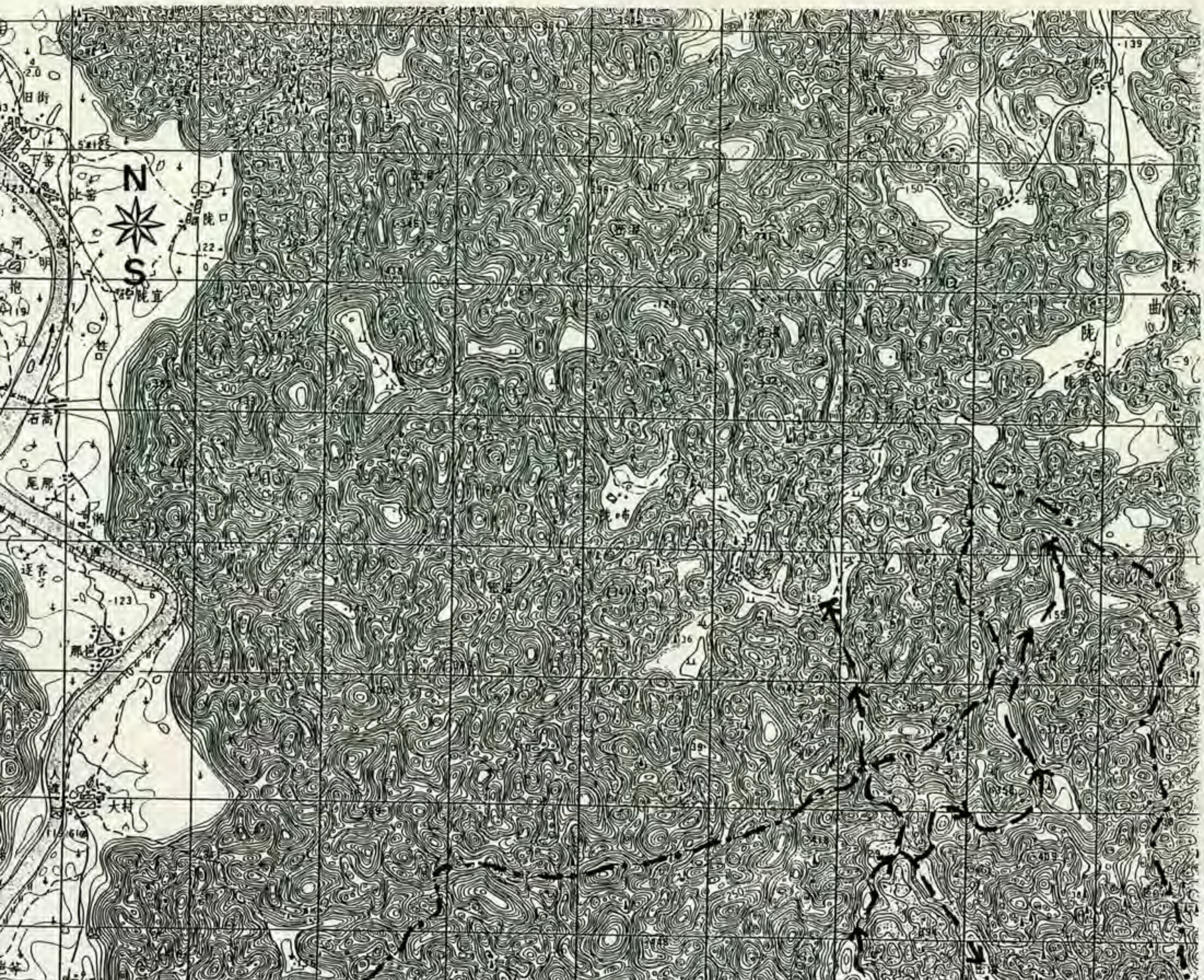
**Figure 2- 3 Working area in Bapen Reserve, showing the hill-groups**

The area of LGS was 35.1km², QN 12km², GF 6km², GP 10km², and MZ 34.3km² (measured on maps scaled 1/10,000). Area in the square was the main study area (detailed in Figure 2-5).

The Longgang Reserve (LGR) was to the southwest of Bapen Reserve, about 107°01'-107°08' E, 22°13'-22°20'N, with elevation ranging from 106 to 518m a.s..l. (*Figure 2- 4*). The mean height of hills was 301m (n = 20), and hills were all interconnected with each other. Only a few trails bordered by cliffs were available for access to valleys inside this reserve. Agricultural work was conducted in a few valleys in peripheral areas. A definite boundary was the Mingjiang River at the west. Boundaries at other sides were arbitrarily defined by the Reserve. The River was the main channel between the Reserve and the outside world. Land transport was not available. There were no villages inside the Reserve. Basically, the habitat has not been fragmented.

### 2.1.5 The main study area

The main study area was located in the central part of LGS in Bapen Reserve (*Plate 2- 2*, *Figure 2- 3* and *Figure 2- 5*), about 22°27'N and 107°52'E (measured at the campsite using GPS 38 Personal Navigator™). It was 532 ha in size and divided into 24 units. A unit was a relatively well-defined natural valley in most cases, but was defined arbitrarily in a few cases (*e.g.*, LGS1-LGS4). Based on the degree of human disturbance and valley closeness, the habitat was scored into four classes. Class I (best quality, given a score of 4) referred to that in which the flat ground still had natural vegetation and the valley was relatively closed and less visited by people. Class II (given a score of 3) referred to that in which the flat land was partly vegetated and not used by farmers, but firewood was sometimes collected by humans. Class III (given a score of 2) referred to that in which farmers used the flat land seasonally, vegetation covered the hill-foot, and firewood was collected more often. Class IV (lowest quality, given a score of 1) was characterised by hill-foot cleared of vegetation, flat land that was used year-round, and a high frequency of firewood collection (almost every day). Each unit was measured using this scoring system and classified into one of four types (*Table 2- 1*). When there was more than one class of habitat in a unit, the class of the larger component was recorded for the unit.



Scale 1:50,000

**Figure 2- 4 Working area in Longgang Reserve where the white-headed langurs occur**

Survey routes are shown in this figure. ---> trail; ---| trail end; _._ Reserve boundary. The boundary marks the area of 20.8km².

**Plate 2- 2 Campsite in LGS.**

This plate shows a research team including the PI, research assistants, and volunteers.

**Plate 2- 3 A pesticide bottle found beside the pond in LY1.**

Such bottles were easily found all over the whole study area. Farmers diluted the pesticide with water in ponds, after which bottles were left beside the ponds. When pond-water rose up, the bottles were sunk into the water and the residual pesticide came out and polluted the water bodies that provided water resources to langurs in the dry season.

**Scale: 1:14285.7**

**Figure 2- 5 The main study area in the valley LGS in Bapen Reserve**

The number in brackets after valley name is the valley unit number (N = 24).
--- trails used in the fieldwork, ---| trail end.

**Table 2- 1 Units and habitat classification of the working area**

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Habitat Class I (45.15ha, 8.5%)** | | | | | | | | | |
| Unit code | LLI1 | LLI4 | LYE | LY3 | LGT | | | | |
| Size (ha) | 8.4 | 8.95 | 6 | 7.5 | 14.3 | | | | |
| **Habitat Class II (57.89ha, 10.9%)** | | | | | | | | | |
| Unit code | LW | LY1 | LY2 | | | | | | |
| Size (ha) | 25.72 | 16.67 | 15.5 | | | | | | |
| **Habitat Class III (163.5ha, 30.7%)** | | | | | | | | | |
| Unit code | LLI2 | LLI3 | LYG | LLGQ | LGQ | LLN | LN | | |
| Size (ha) | 4.5 | 23.65 | 16.05 | 4.5 | 33.7 | 29.6 | 51.5 | | |
| **Habitat Class IV (265.46ha, 49.9%)** | | | | | | | | | |
| Unit code | LB | LGS1 | LGS2 | LGS3 | LGS4 | LWG | LL | LH | LG |
| Size (ha) | 16.53 | 17.3 | 15.75 | 18.15 | 11.69 | 32 | 73.65 | 44.54 | 35.85 |

Note: 1. The size was measured from the shaded area on maps of 1/5000 in scale. The units are also indicated on Figure 2-5. When the habitat classes were used for comparisons with other ecological factors, Habitat Class I was scored as 4, II as 3, III as 2, and IV as 1 to indicate the habitat quality.

Lack of surface water is a typical feature of the karst topography in Southwest Guangxi. There were 12 seasonal ponds where water accumulated from April to September. The water was available until January of the following year; thus the ponds may be important resources to langurs during the relatively dry season from October to January. However, because of agricultural work, the water was polluted by disposal of pesticide bottles (See *Plate 2- 3*).

Detailed data on the ecology of the main study area have been collected. There were no previous data on climate applicable to this research; thus climatic information was also collected during the fieldwork and will be detailed before vegetation is described below.

## 2.2 Methods

### 2.2.1 Climate

Data, including relative humidity, rainfall, and max and min temperatures, were collected in Bapen Reserve from 2100 hrs on September 15, 1997, to 1030 hrs on September 13, 1998, lasting 364 days. Daily readings were recorded at 2100 hrs at the Reserve Station in September 1997 and at the campsite after that. The Station was 6 km away from the campsite.

### 2.2.2 Vegetation

#### *2.2.2.1 Distribution of vegetation patches*

A survey was conducted of vegetation patches in four hill-groups in Bapen Reserve from September 1996 to April 1997. A vegetation patch was defined as a continuous forest patch on a cliff or hill-foot slope. Thus the size of each patch and the distance between patches could be very small. Langurs could move freely across them. The researcher surveyed hills by pacing, locating vegetation patches by sight and drawing them on maps of 1/10,000 in scale.

Another survey was carried out of the vertical distribution of vegetation patches in the five hill-groups in Bapen and in LGR during the same period. A hill was not covered with vegetation everywhere; instead, rock was exposed in some places (see *Plate 2- 4*). Also, vegetation was taller and denser in some places and shorter and more open at other places. To characterise the distribution pattern, five categories were established: *bare rock (BR), grass (GR), open (short) bush (OB), dense (tall) bush (DB),* and *tall tree forest (TT). A sample* was made on a hill-aspect. The height was divided into *top (T), upper (U), halfway (M), lower (L),* and *hill-foot (H)*. Each vegetation category at each height level was recorded, and its proportion in area was estimated. Sample hills were predetermined on maps by selecting them evenly from the hills in a hill-group without bias between the north and south, the east and west, and the central and peripheral areas. Number of samples depended on toughness of terrain and the distance that the researcher had to walk.

#### *2.2.2.2 Species composition*

This work was carried out in the main study area in March and April 1998. In each unit (*Table 2- 1*), samples were made on the ground and slope every 50 m along the edge between bush and cultivated land. At each sample site, a sample rope was pulled from the edge to the hill-foot. Length varied with distance between the edge

**Plate 2- 4 Vegetation distribution at vertical levels of a hill-aspect.**

On this hill-aspect, there were a patch of DB (patch 1) and a patche of OB (patch 2). The area of the hill-aspect was 100%, 45% of which was covered by *DB* (dense bush); 1/3 of the *DB* was located at *Lower* (level-*L*), and 2/3 at *Hill-foot* (level-*H*), so *DB* at *H* was 30% and *DB* at *L* was 15%. 10% of the area was *BR* (bald rock, patch 3); 1/2 of the *BR* was at *Half-way* (level-*M*), 1/4 at *L*, and 1/4 at *Upper* (level-*U*), so *BR* at *L* was 2.5%, *BR* at *M* 5%, and *BR* at *U* 2.5%. The remaining 45% was covered by *OB* (open bush), 1/10 of the *OB* was at *L*, 3/10 at *M*, 3/10 at *U*, and 3/10 at the *Top* (level-*T*), so *OB* at *L* was 4.5%, *OB* at *M* 13.5%, *OB* at *U* 13.5%, and *OB* at *T* 13.5%. No *GR* (grass) and *TT* (tall tree) were found here. In a checksheet, the records would be as follows: A. *BR*-10% (2.5% at L + 5% at M + 2.5% at U); B. *GR* - 0%; C. *OB* - 45% (4.5% at L + 13.5% at M + 13.5% at U + 13.5% at T); D. *DB* - 45% (30% at H + 15% at L); E. *TT* - 0%. In the final data processing, percentages of each category at each height level from a hill-group were averaged to give data shown in Figure 2-6. To reduce variation from different viewing angles, the observer always stood at the centre of the dimension from left to right.

and the hill-foot cliff, but the maximum length was 50m. Trees and woody lianas ≥ 1.2cm dbh within 5m to either side of the rope were identified and recorded. The lower limit of 1.2cm was determined, because langurs had been seen in trees of this size and larger.

There are a number of indices that may be used to calculate species diversity (Ricklefs, 1990). There are advantages and disadvantages to using different indices and therefore often more than one index is used to assess species diversity. For comparisons with other studies, the Shannon-Weaver Diversity Index and Simpson's Diversity Index were used in this study. The Shannon-Weaver Index is sensitive to sample size (Rasmussen, 1980). It is calculated as follows:

$$\mathbf{H' = \sum P_{\mathit{i}} \times \ln P_{\mathit{i}}} \qquad \textbf{Shannon-Weaver Index}$$

where $P_i$ is the proportion of individuals found in the *i*th species. This index is designed to assess the variation in the number of species as well as variation in the number of individuals within each species.

Simpson's Index is less sensitive to sample size (Magurran, 1955). According to most other studies in which both Shannon-Weaver Index and the Simpson's Index were considered (e.g., White, 1992), the Simpson's Index was also used as an index of diversity in the present study. It is calculated as follows:

$$\mathbf{D = 1/\sum P_{\mathit{i}}^2} \qquad \textbf{Simpson's Index}$$

where $P_i$ is also the proportion of individuals found in the *i*th species, the same as that in the Shannon-Weaver Index.

Because a plant community with few, evenly represented species can have the same diversity index as one with many, unevenly represented species, an index of evenness is also required. The J' of Pielou (Pielou, 1975) is an index frequently used as an index of evenness. It is calculated by dividing the Shannon-Weaver Index using the hypothetical maximum diversity, as follows:

$$\mathbf{J' = H' / Hmax} \qquad \textbf{J' of Pielou}$$

where Hmax = lnS, where S is equal to the total number of species in the unit of interest.

The Coefficient of Dispersion (Greig-Smith, 1983) gives an indication of departure from random for the distribution of a particular tree species. If a species is dispersed randomly in a Poisson distribution, the Coefficient is 1. A coefficient of less than 1 suggests a regular, over-dispersed distribution and if greater than 1, a clumped pattern. It is calculated as follows:

$\frac{\sum(x-m)^2}{m}$ or **(variance/mean)×(number of observations - 1) Index of Dispersion**

where x is the number of individuals of a species in each sample, and m the mean. Significance is assessed by reference to the table of $\chi^2$, the observed value of the index of dispersion being entered in the table. As it can only be calculated for species that are neither very rare nor very common (Greig-Smith, 1983), the following trees were excluded from the calculations: *Broussonetia kazinoki* (Moraceae), *Mappianthus iodoides* (Icacinaceae), *Pueraria thunbergiana* (Papilionaceae), and *Tetraceae asiatica* (Dilleniaceae). *Cuscuta chinensis* (Convolvulaceae) and *Madhuca pasquieri* (Sapotaceae) were also excluded, because the former species was a parasitic vine, so data were not collected from it, and the latter species was not encountered during the survey.

A standard sample size was 10m x 50m, but the length of 50 m was not always available because of anthropogenic vegetation clearance. It was assumed that individuals of a species were evenly distributed in a sample. Thus data from the samples < 50m long were converted proportionally, and the converted data are entered for calculations.

An index, *ratio of species/family,* was defined using the number of species divided by the number of families to indicate the uniqueness of the vegetation. The higher the ratio, the less the uniqueness, because a higher ratio indicates more species belonging to the same families. Another index, *ratio of indv./area* was defined as the percentage of individuals divided by the percentage of area to assess differentiation in the distribution of species in different habitat classes.

### *2.2.2.3 Phenology*

There are three methods that have been widely used by different researchers in order to quantify variations in the production of plant parts and their availability. They are (1) recording the number of trees with fruit each month (Gautier-Hion *et al.*, 1985), (2) systematically counting or weighing fallen fruits (Terborgh, 1983), and (3) estimating the crop size for individual trees as a proportion of the maximum potential score for that species (Homewood, 1978). White-headed langurs ate large quantities of leaves, so data on leaf phenological phases were important in the ecology of langurs; thus the third method was used in the present study.

Before data collection, a coding system of food plant species had been established according to Lai (1987) and local people who had experience of the langur diet. There were 39 plant species in this coding system. Each species was coded with a number. Species 39 was excluded from the system in September 1997, because it was a domestic plant and eaten by langurs in captivity not in the wild. Species 36 and 38 were excluded in October, because they were eaten by langurs in captivity only and were not found in the main study area. During observation of feeding ecology, eight new species were added later on by April 1998, after which no new species was added. Species 42 had only one individual found and tagged. It died in February 1998.

Searching was carried out along the hill-foot, trails, on the hilltop, and on cliffs, and tagging was opportunistic initially. A maximum of ten individuals was tagged for each species. Thereafter, the tagged plants were visited once per month according to the established sequence. Each plant was scored in terms of relative quantity of food item on a 4-point scale where 4 was maximum abundance. For leaves, there were 3 categories: *young leaves, mature leaves,* and *senescing leaves.* For flowers, there were 2 classes: *flower bud* and *open flower*. Fruits were divided into *immature fruits* and *mature fruits*.

### 2.2.3 Statistical techniques

With reference to Fowler and Cohen (1992), the Spearman Rank Correlation Coefficient was used to assess the influences of climatic factors on phenological patterns, and the relationship between habitat types and plant species diversity.

## 2.3 Results

### 2.3.1 Climate

The highest temperature was 38 ° C in April and July 1998, the lowest 5 ° C in January, and the mean temperature 22 ° C. Air humidity ranged from 39% to 98% and the mean was 85%. The greatest daily rainfall was 80mm, the total was 1167.7mm with a rainy season beginning in April and ending in early September. The mean daily rainfall was 3.2 mm. *Figure 2- 6* shows details of the climatic changes.

Four seasons were recognised: spring, summer, autumn, and winter. According to the mean temperature, March was spring, because the air temperature was increasing. Summer started in April and ended in August, during which the air temperature maintained a high level. Autumn started in September and ended in November, during which the air temperature was decreasing. Winter was from December to February, because the air temperature was at the lowest level during this period.

The rainfall and humidity curves (*Figure 2- 6*) showed that the air humidity did not always keep pace with the rainfall. The air humidity decreased to the lowest in April 1998. Rain water accumulated in the seasonal ponds during the rainy season in summer 1997. It disappeared completely in April 1998. It was apparent that rainwater in these ponds played an important role in maintaining the air humidity. It rained little during the whole winter. Langurs living on limestone hills might have difficulty obtaining water from places outside these seasonal ponds. It was found from the behavioural observations that white-headed langurs came to the ground to drink water from these ponds in the winter (detailed in Chapter V). Thus, these water bodies appeared to be important resources for langurs.

### 2.3.2 Vegetation

#### *2.3.2.1 Distribution*

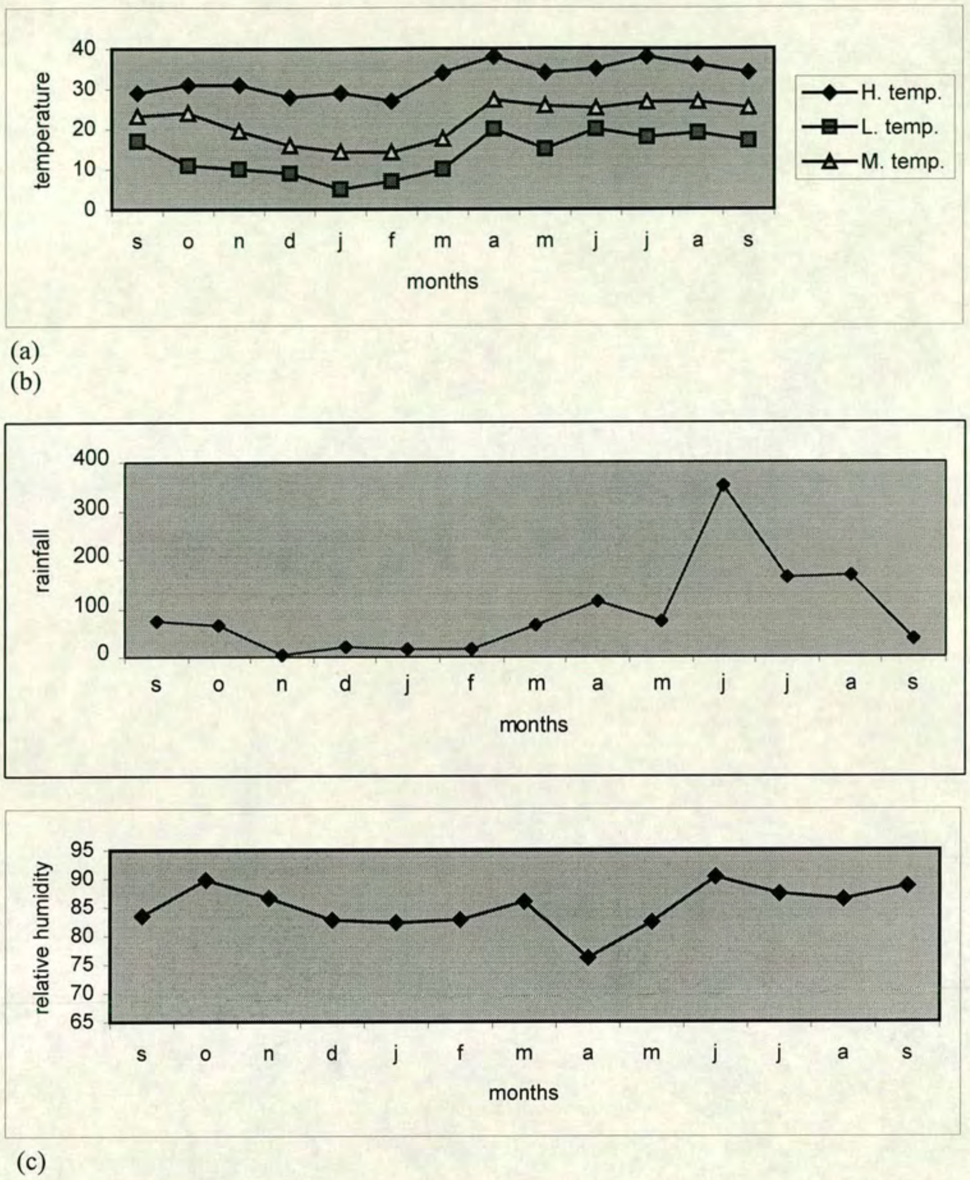


**Figure 2- 6 Climatic changes from Sept. 1997 to Sept. 1998**

(a) temperature (°C), (b) monthly rainfall (mm), and (c) monthly mean air humidity (%). X-axes indicate months.

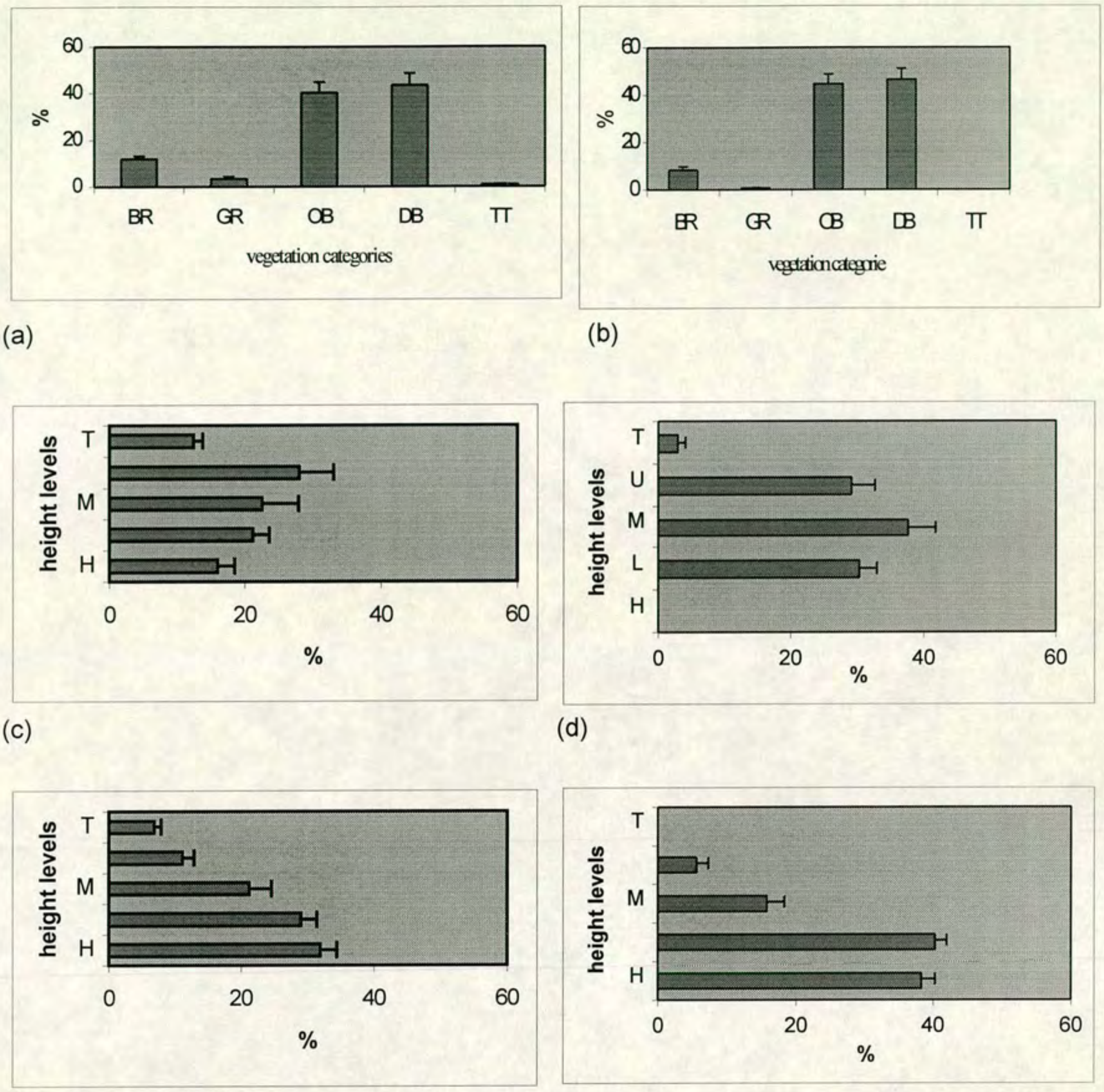
There were 2,452 vegetation patches surveyed. *Table 2- 2* shows summary information. These patches were largely restricted to hills, and were in general very small in size. It was easy for langurs to traverse them freely. Thus, a *habitat fragment* was defined as a hill or an area of connected hills where langurs could move about freely. Fragment size depended on interconnectedness of hills; a fragment composed of several connected hills was larger in size than a fragment composed of one hill. Table 2- 2indicates that LGS was the best habitat among the four hill-groups. This is because *a)* a comparison with MZ (which was similar in area to LGS) showed that the vegetation was less fragmented, and *b)* there were more dense bush patches than open bush and grass slope patches in LGS, whereas the reverse was true in the other three hill-groups.

**Table 2- 2 Distribution of vegetation patches in the working area**

| Hill-Group | Hill-aspects | Area (ha) | No. Vegetation Patches | | |
|---|---|---|---|---|---|
| | | | A (ratio) | B (ratio) | Total |
| Bapen R. | | | | | |
| QN | 15 | 20.9 | 197(9.4) | 204(9.8) | 401 |
| LGS | 15 | 20.4 | 401(19.7) | 182(8.9) | 583 |
| MZ | 15 | 22.1 | 462(20.9) | 638(28.9) | 1100 |
| GF | 15 | 31.6 | 186(5.9) | 272(8.6) | 458 |
| GP | 15 | 31.1 | | | |
| Longgang R. | | | | | |
| LGR | 30 | 51.9 | | | |
| Total | 105 | 178.1 | 1246 | 1296 | 2542 |

A: No. of dense bush (DB) patches; B: No. of open bush (OB) and grass slope patches. Ratios indicate the number of vegetation patches in an area of 1 ha.

During the survey on vertical distribution of vegetation patches, 105 hill aspects were surveyed. Summary information is shown in *Table 2- 2*. *Figure 2- 7* shows the proportions of the five categories in area and the distribution of DB and OB at different height levels. Composition of the five categories in general (left column of *Figure 2- 7*) was similar to that in LGS (right column). The general pattern of vegetation distribution was that there was more vegetation at lower levels than at higher levels. Also, due to a difference in water availability, tallness of vegetation decreased with altitude. Compared to dense bush, open bush was a



(a) (b)

(c) (d)

(e) (f)

**Figure 2- 7 Proportions and vertical distribution of vegetation patches in the five hill-groups (a, c, e), and in LGS (b, d, f).**

BR = bare rock, GR = grass, OB = open bush, DB = dense bush, TT = tall tree, T = hill-top, U = upper level, M = halfway, L = lower level, and H = hill-foot. (a) and (b) indicate the percentage of the five categories; (c) and (d) the open bush, and (e) and (f) the dense bush.

product of human disturbance at the hill-foot and on the flat ground. However, distribution of OB and DB in LGS was different from the general pattern, because there was little open bush left on the hill-foot due to vegetation clearance. In valleys that had been less disturbed by humans in LGS, the hill-foot was covered with long and dense bush; whereas in valleys more accessible to humans, vegetation at the hill-foot was cleared and lost to agricultural use. Vegetation cover on the top of hills might be under-estimated, because surveys were done from the base of cliffs, and it was usually impossible to see the whole top surface. However, where it had been possible to climb up, it was found that the top of hills was covered by thorny short vegetation that was sparsely distributed. Bare rock occupied a large proportion of the area. To partly reduce the extent of under-estimation, surveying of hill aspects was done from a distance of about 200 - 300m. So it is assumed that the distribution pattern shown in *Figure 2- 7* was largely consistent with the actual situation.

### *2.3.2.2 Species richness*

Three-hundred and eleven transects were sampled in an area of 11.603ha. A total of 13,204 plants were recorded, belonging to 164 species plus 2 variations (112 genera) from 48 families (*Table 2- 3*). The ratio of species/family was 3.42. *Table 2- 4* shows summary sampling information in each unit and Appendix A shows the species encountered and their abundance.

The relationship between area surveyed and species richness is shown in *Figure 2- 8*. Two points have been demonstrated: 1) the species-area curve is biphasic, which indicates ecological heterogeneity, and 2) the curve has levelled off above 9ha, thus sample size was large enough for describing the plant community. *Table 2- 5* shows species diversity in each unit. Area with higher degree of disturbance was larger than that with lower degree, which may be the cause of a correlation between disturbance and area (Spearman Rank $r_S = 0.483$, two-tailed, $p < 0.05$). Because diversity (the Shannon-Weaver Index) was significantly influenced by area surveyed (Pearson $r = 0.492$, $p < 0.05$), two ratios were derived from the Sannon-Weaver Index, the Simpson Index, and the area surveyed in this table to explore the relationship between plant diversity and habitat quality. Because rare

**Table 2- 3 Distribution of plant species among habitat classes (Code: food plant species no., * top 15 food plant species)**

| Family/Species | Total | Habitat Classse | | | | | | | | Code |
|---|---|---|---|---|---|---|---|---|---|---|
| | | I | | II | | III | | IV | | |
| ALANGIACEAE (527 indv., 1 sp., 1 gen.) | | No | % | No | % | No | % | No | % | |
| *Alangium chinense* | 527 | 5 | 0.9 | 122 | 23.1 | 206 | 39.1 | 194 | 36.8 | |
| ANACARDIACEAE (405 indv., 3 spp., 3 gen.) | | | | | | | | | | |
| *Pegia bijugu* | 27 | 6 | 22.2 | 2 | 7.4 | 9 | 33.3 | 10 | 37.0 | |
| *Pistacia weinmannifolia* | 71 | 10 | 14.1 | 2 | 2.8 | 4 | 5.6 | 55 | 77.5 | 46 |
| *Rhus chinensis* | 307 | 0 | 0.0 | 18 | 5.9 | 120 | 39.1 | 169 | 55.0 | |
| ANNONACEAE (220 indv., 5 spp., 4 gen.) | | | | | | | | | | |
| *Dasymaschalon trichophorum* | 1 | 0 | 0.0 | 1 | 100.0 | 0 | 0.0 | 0 | 0.0 | |
| *Desmos cochinchinensis* | 202 | 16 | 7.9 | 32 | 15.8 | 26 | 12.9 | 128 | 63.4 | |
| *Fissistigma chloroneurum* | 5 | 5 | 100.0 | | 0.0 | 0 | 0.0 | 0 | 0.0 | |
| *F. retusum* | 7 | 5 | 71.4 | | 0.0 | 0 | 0.0 | 2 | 28.6 | |
| *Polyalthia plagioneura* | 5 | 0 | 0.0 | 5 | 100.0 | 0 | 0.0 | 0 | 0.0 | |
| APORYNACEAE (16 indv., 4 spp., 3 gen.) | | | | | | | | | | |
| *Rauvolfia verticillata* | 5 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 5 | 100.0 | |
| *Strophanthus divericatus* | 2 | 0 | 0.0 | 0 | 0.0 | 2 | 100.0 | 0 | 0.0 | |
| *Wrightia hainanensis* | 4 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 4 | 100.0 | |
| *W. pubescens* | 5 | 0 | 0.0 | 3 | 60.0 | 0 | 0.0 | 2 | 40.0 | |
| ARALIACEAE (71 indv., 3 spp., 3 gen.) | | | | | | | | | | |
| *Heteropanax fragrans* | 10 | 6 | 60.0 | 0 | 0.0 | 4 | 40.0 | 0 | 0.0 | |
| *Schefflera arboricola* | 30 | 0 | 0.0 | 0 | 0.0 | 9 | 30.0 | 21 | 70.0 | |
| *Tetrapanax papyriferus* | 31 | 11 | 35.5 | 0 | 0.0 | 20 | 64.5 | 0 | 0.0 | |
| ASCLEPIADACEAE (3 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Cryptolepis buchanani* | 3 | 0 | 0.0 | 0 | 0.0 | 1 | 33.3 | 2 | 66.7 | 11 |
| BIGNONIACEAE (842 indv., 3 spp., 3 gen.) | | | | | | | | | | |
| *Oroxylun indicum* | 783 | 1 | 0.1 | 25 | 3.2 | 490 | 62.6 | 267 | 34.1 | 4 |
| *Radermachera si* | 29 | 2 | 6.9 | 1 | 3.4 | 12 | 41.4 | 14 | 48.3 | |
| *Stereospermum chelonoides* | 30 | 1 | 3.3 | 0 | 0.0 | 4 | 13.3 | 25 | 83.3 | |
| BOMBACACEAE (64 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Gossampinus malabarica* | 64 | 0 | 0.0 | 5 | 7.8 | 46 | 71.9 | 13 | 20.3 | |
| BORAGINACEAE (4 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Cordia dichotoma* | 4 | 0 | 0.0 | 2 | 50.0 | 0 | 0.0 | 2 | 50.0 | |
| CAESALPINIACEAE (209 indv., 10 spp., 3 gen.) | | | | | | | | | | |
| *Bauhinia brachycarpa var. cavaleriei* | 8 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 8 | 100.0 | |
| *B. championi* | 54 | 1 | 1.9 | 2 | 3.7 | 12 | 22.2 | 39 | 72.2 | |
| *B. erythropoda* | 2 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 2 | 100.0 | |
| *Caesalpinia aestivalis* | 49 | 0 | 0.0 | 0 | 0.0 | 3 | 6.1 | 46 | 93.9 | |
| *C. decapetala* | 33 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 33 | 100.0 | |
| *C. minax* | 6 | 0 | 0.0 | 1 | 16.7 | 0 | 0.0 | 5 | 83.3 | |
| *C. nuga* | 5 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 5 | 100.0 | |
| *C. sappan* | 4 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 4 | 100.0 | 51 |
| *C. vernalis* | 5 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 5 | 100.0 | |
| *Zenia insignis* | 38 | 0 | 0.0 | 0 | 0.0 | 1 | 2.6 | 37 | 97.4 | 17 |
| CAPPARIDACEAE (13 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Capparis viminea* | 13 | 6 | 46.2 | 0 | 0.0 | 0 | 0.0 | 7 | 53.8 | 1* |
| CAPRIFOLIACEAE (7 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Sambucus racemosa* | 7 | 7 | 100.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | |

Table 2-3 (continued-1)

| Family/Species | Total | Habitat Classse | | | | | | | | Code |
|---|---|---|---|---|---|---|---|---|---|---|
| | | I | | II | | III | | IV | | |
| CELASTRACEAE (2 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Euonymus laxiflorus* | 2 | 2 | 100.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | |
| COMBRETACEAE (9 indv., 2 spp., 1 gen.) | | | | | | | | | | |
| *Combretum alfredii* | 8 | 4 | 50.0 | 0 | 0.0 | 4 | 50.0 | 0 | 0.0 | |
| *C. incertum* | 1 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 1 | 100.0 | |
| DILLENIACEAE (6 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Tetraceae asiatica* | 6 | 0 | 0.0 | 0 | 0.0 | 6 | 100.0 | 0 | 0.0 | 32* |
| EBENACEAE (22 indv., 2 spp., 1 gen.) | | | | | | | | | | |
| *Diospyros dumetorum* | 2 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 2 | 100.0 | |
| *D. siderophyllus* | 20 | 5 | 25.0 | 0 | 0.0 | 8 | 40.0 | 7 | 35.0 | |
| EUPHORBIACEAE (2414 indv., 21 spp. + 1 var., 13 gen.) | | | | | | | | | | |
| *Alchornea rugosa* | 225 | 5 | 2.2 | 1 | 0.4 | 59 | 26.2 | 160 | 71.1 | |
| *A. trewioides* | 16 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 16 | 100.0 | |
| *Aporosa chinensis* | 1 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 1 | 100.0 | |
| *Bischofia racemosa* | 102 | 28 | 27.5 | 13 | 12.7 | 47 | 46.1 | 14 | 13.7 | |
| *Breynia fruticosa* | 3 | 0 | 0.0 | 0 | 0.0 | 1 | 33.3 | 2 | 66.7 | 34 |
| *B. hyposauropus* | 8 | 0 | 0.0 | 0 | 0.0 | 6 | 75.0 | 2 | 25.0 | |
| *Bridelia monoica* | 19 | 0 | 0.0 | 0 | 0.0 | 8 | 42.1 | 11 | 57.9 | |
| *Croton kwangsiensis* | 212 | 3 | 1.4 | 19 | 9.0 | 46 | 21.7 | 144 | 67.9 | |
| *Drypetes integrifolia* | 9 | 0 | 0.0 | 0 | 0.0 | 8 | 88.9 | 1 | 11.1 | |
| *D. tonkinensis* | 8 | 8 | 100.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | |
| *Endospermum chinense* | 5 | 4 | 80.0 | 0 | 0.0 | 0 | 0.0 | 1 | 20.0 | |
| *Fluggea virosa* | 594 | 38 | 6.4 | 101 | 17.0 | 197 | 33.2 | 258 | 43.4 | 10 |
| *Glochidion lanceolarum* | 25 | 0 | 0.0 | 5 | 20.0 | 12 | 48.0 | 8 | 32.0 | |
| *G. philippinense* | 51 | 1 | 2.0 | 0 | 0.0 | 5 | 9.8 | 45 | 88.2 | |
| *G. puberum* | 2 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 2 | 100.0 | |
| *1) Mallotus apelta* | 8 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 8 | 100.0 | |
| *2) M. a. var. kwangsiensis* | 404 | 4 | 1.0 | 94 | 23.3 | 167 | 41.3 | 139 | 34.4 | |
| *M. philippinensis* | 487 | 2 | 0.4 | 37 | 7.6 | 199 | 40.9 | 249 | 51.1 | |
| *M. repandus* | 36 | 0 | 0.0 | 2 | 5.6 | 1 | 2.8 | 33 | 91.7 | |
| *Phyllanthus emblica* | 134 | 2 | 1.5 | 2 | 1.5 | 52 | 38.8 | 78 | 58.2 | |
| *P. reticulata* | 5 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 5 | 100.0 | 49 |
| *Sapium discolor* | 51 | 0 | 0.0 | 10 | 19.6 | 22 | 43.1 | 19 | 37.3 | |
| FLACOURTIACEAE (1 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Xylosma congestum* | 1 | 0 | 0.0 | 0 | 0.0 | 1 | 100.0 | 0 | 0.0 | |
| GNETACEAE (2 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Gnetum montanum* | 2 | 0 | 0.0 | 0 | 0.0 | 2 | 100.0 | 0 | 0.0 | 44 |
| HAMAMELIDACEAE (75 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Liquidambar fomosana* | 75 | 23 | 30.7 | 9 | 12.0 | 23 | 30.7 | 20 | 26.7 | |
| HYPERICACEAE (144 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Cratoxylon ligustrinum* | 144 | 4 | 2.8 | 21 | 14.6 | 49 | 34.0 | 70 | 48.6 | |
| ICACINACEAE (14 indv., 2 spp.+ 1 var., 2 gen.) | | | | | | | | | | |
| *1) Iodes ovalis* | 7 | 0 | 0.0 | 0 | 0.0 | 3 | 42.9 | 4 | 57.1 | |
| *2) I. o. var. vitiginea* | 1 | 0 | 0.0 | 0 | 0.0 | 1 | 100.0 | 0 | 0.0 | 55 |
| *Mappianthus iodoides* | 6 | 2 | 33.3 | 0 | 0.0 | 0 | 0.0 | 4 | 66.7 | 28* |
| LAURACEAE (1419 indv., 4 spp., 2 gen.) | | | | | | | | | | |
| *Lindera communis* | 418 | 151 | 36.1 | 107 | 25.6 | 90 | 21.5 | 70 | 16.7 | 20* |
| *L. pulcherrima var. attenuata* | 504 | 453 | 89.9 | 0 | 0.0 | 51 | 10.1 | 0 | 0.0 | |

Table 2-3 (continued-2)

| Family/Species | Total | Habitat Classse | | | | | | | | Code |
|---|---|---|---|---|---|---|---|---|---|---|
| | | I | | II | | III | | IV | | |
| *Litsea euosma* | 443 | 8 | 1.8 | 10 | 2.3 | 140 | 31.6 | 285 | 64.3 | 9 |
| *L. monopetala* | 64 | 8 | 12.5 | 9 | 14.1 | 44 | 68.8 | 3 | 4.7 | |
| LOGANIACEAE (65 indv., 2 spp., 1 gen.) | | | | | | | | | | |
| *Buddlera lindleyans* | 2 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 2 | 100.0 | |
| *B. madacascariensis* | 63 | 0 | 0.0 | 4 | 6.3 | 13 | 20.6 | 46 | 73.0 | |
| MELIACEAE (689 indv., 5 spp., 4 gen.) | | | | | | | | | | |
| *Chukrasia tabularis* | 1 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 1 | 100.0 | |
| *Cipadessa cinerascens* | 640 | 5 | 0.8 | 95 | 14.8 | 256 | 40.0 | 284 | 44.4 | |
| *Melia azedarach* | 4 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 4 | 100.0 | |
| *Toona sinensis* | 9 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 9 | 100.0 | |
| *T. sureni var. pubescens* | 35 | 6 | 17.1 | 0 | 0.0 | 21 | 60.0 | 8 | 22.9 | 27 |
| MENISPERMACEAE (7 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Cocculus laurifolius* | 7 | 3 | 42.9 | 0 | 0.0 | 4 | 57.1 | 0 | 0.0 | |
| MIMOSACEAE (552 indv., 5 spp., 4 gen.) | | | | | | | | | | |
| *Adenanthera chinensis* | 9 | 0 | 0.0 | 0 | 0.0 | 8 | 88.9 | 1 | 11.1 | |
| *A. pavonina* | 12 | 0 | 0.0 | 0 | 0.0 | 10 | 83.3 | 2 | 16.7 | |
| *Albizzia kalkora* | 477 | 16 | 3.4 | 38 | 8.0 | 177 | 37.1 | 246 | 51.6 | |
| *Leucaena glauca* | 9 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 9 | 100.0 | |
| *Pithecellobium clypearia* | 50 | 0 | 0.0 | 4 | 8.0 | 0 | 0.0 | 46 | 92.0 | 12* |
| MORACEAE (1289 indv., 16 spp., 4 gen.) | | | | | | | | | | |
| *Broussonetia kazinoki* | 4 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 4 | 100.0 | 22* |
| *B. papyrifera* | 211 | 4 | 1.9 | 27 | 12.8 | 60 | 28.4 | 120 | 56.9 | |
| *Cudrania cochinchinensis* | 398 | 10 | 2.5 | 71 | 17.8 | 189 | 47.5 | 128 | 32.2 | 6 |
| *C. tricuspidata* | 5 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 5 | 100.0 | |
| *Ficus altissima* | 4 | 0 | 0.0 | 0 | 0.0 | 2 | 50.0 | 2 | 50.0 | 37 |
| *F. elastica* | 8 | 2 | 25.0 | 0 | 0.0 | 1 | 12.5 | 5 | 62.5 | |
| *F. gibbosa* | 184 | 7 | 3.8 | 34 | 18.5 | 50 | 27.2 | 93 | 50.5 | 50 |
| *F. glabberrima* | 72 | 29 | 40.3 | 7 | 9.7 | 24 | 33.3 | 12 | 16.7 | |
| *F. harmandii* | 46 | 8 | 17.4 | 9 | 19.6 | 8 | 17.4 | 21 | 45.7 | |
| *F. hispida* | 134 | 54 | 40.3 | 6 | 4.5 | 54 | 40.3 | 20 | 14.9 | |
| *F. microcarpa* | 12 | 0 | 0.0 | 6 | 50.0 | 4 | 33.3 | 2 | 16.7 | 26* |
| *F. nervosa* | 5 | 1 | 20.0 | 0 | 0.0 | 3 | 60.0 | 1 | 20.0 | 13 |
| *F. parvifolia* | 12 | 1 | 8.3 | 2 | 16.7 | 2 | 16.7 | 7 | 58.3 | |
| *F. subulata* | 5 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 5 | 100.0 | |
| *F. taiwaniana* | 190 | 111 | 58.4 | 10 | 5.3 | 42 | 22.1 | 27 | 14.2 | |
| *Meras australis* | 28 | 0 | 0.0 | 0 | 0.0 | 22 | 78.6 | 6 | 21.4 | 14 |
| MYRSINACEAE (211 indv., 4 spp., 3 gen.) | | | | | | | | | | |
| *Ardisia depressa* | 199 | 164 | 82.4 | 0 | 0.0 | 35 | 17.6 | 0 | 0.0 | |
| *Embelia ribes* | 1 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 1 | 100.0 | |
| *Maesa japonica* | 2 | 0 | 0.0 | 0 | 0.0 | 2 | 100.0 | 0 | 0.0 | |
| *M. montana* | 9 | 0 | 0.0 | 0 | 0.0 | 4 | 44.4 | 5 | 55.6 | |
| MYRTACEAE (262 indv., 2 spp., 2 gen.) | | | | | | | | | | |
| *Psidium guajava* | 174 | 2 | 1.1 | 20 | 11.5 | 11 | 6.3 | 141 | 81.0 | |
| *Syzygium cumini* | 88 | 4 | 4.5 | 16 | 18.2 | 23 | 26.1 | 45 | 51.1 | |
| OLEACEAE (35 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Ligustrum sinensis* | 35 | 3 | 8.6 | 0 | 0.0 | 5 | 14.3 | 27 | 77.1 | |
| OPILIACEAE (178 indv., 2 spp., 2 gen.) | | | | | | | | | | |
| *Cansjera rheedii* | 177 | 28 | 15.8 | 9 | 5.1 | 65 | 36.7 | 75 | 42.4 | 23 |
| *Lepioncerus latisquamus* | 1 | 0 | 0.0 | 0 | 0.0 | 1 | 100.0 | 0 | 0.0 | |

Table 2-3 (continued-3)

| Family/Species | Total | Habitat Classse | | | | | | | | Code |
|---|---|---|---|---|---|---|---|---|---|---|
| | | I | | II | | III | | IV | | |
| PAPILIONACEAE (261 indv., 10 spp., 5 gen.) | | | | | | | | | | |
| *Cladrastis platycarpa* | 5 | 5 | 100.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | |
| *Dalbergia cavaleriei* | 4 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 4 | 100.0 | |
| *D. hancei* | 62 | 12 | 19.4 | 0 | 0.0 | 27 | 43.5 | 23 | 37.1 | |
| *D. hupeana* | 10 | 0 | 0.0 | 3 | 30.0 | 2 | 20.0 | 5 | 50.0 | |
| *D. pinnata* | 1 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 1 | 100.0 | |
| *Desmodium eleguns* | 15 | 0 | 0.0 | 0 | 0.0 | 3 | 20.0 | 12 | 80.0 | |
| *Millettia nitida* | 6 | 2 | 33.3 | 0 | 0.0 | 4 | 66.7 | 0 | 0.0 | |
| *M. pachycarpa* | 140 | 24 | 17.1 | 8 | 5.7 | 85 | 60.7 | 23 | 16.4 | 29* |
| *M. tsui* | 2 | 0 | 0.0 | 0 | 0.0 | 2 | 100.0 | 0 | 0.0 | |
| *Pueraria thunbergiana* | 7 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 7 | 100.0 | 16* |
| PENTAPHYLACACEAE (13 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Pentaphylax euryoides* | 13 | 0 | 0.0 | 10 | 76.9 | 3 | 23.1 | 0 | 0.0 | |
| RHAMNACEAE (13 indv., 3 spp., 2 gen.) | | | | | | | | | | |
| *Rhamnus leptophylla* | 2 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 2 | 100.0 | |
| *Sageretia hamosa* | 3 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 3 | 100.0 | 8 |
| *S. theejans* | 8 | 0 | 0.0 | 3 | 37.5 | 3 | 37.5 | 2 | 25.0 | |
| ROSACEAE (4 indv., 2 spp., 2 gen.) | | | | | | | | | | |
| *Prumus persica* | 2 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 2 | 100.0 | |
| *Pyrus calleryana* | 2 | 1 | 50.0 | 0 | 0.0 | 1 | 50.0 | 0 | 0.0 | |
| RUBIACEAE (125 indv., 4 spp., 4 gen.) | | | | | | | | | | |
| *Adina racemosa* | 61 | 14 | 23.0 | 5 | 8.2 | 3 | 4.9 | 39 | 63.9 | |
| *Lasianthus chinensis* | 21 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 21 | 100.0 | |
| *Randia spinosa* | 42 | 1 | 2.4 | 9 | 21.4 | 25 | 59.5 | 7 | 16.7 | |
| *Tarenna depauperata* | 1 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 1 | 100.0 | |
| RUTACEAE (409 indv., 6 spp., 4 gen.) | | | | | | | | | | |
| *Clausena dunniana var. henryi* | 8 | 0 | 0.0 | 2 | 25.0 | 0 | 0.0 | 6 | 75.0 | |
| *C. emarginata* | 3 | 0 | 0.0 | 0 | 0.0 | 3 | 100.0 | 0 | 0.0 | |
| *C. excavata* | 277 | 10 | 3.6 | 55 | 19.9 | 127 | 45.8 | 85 | 30.7 | 21 |
| *Glycosmis citrifolia* | 16 | 5 | 31.3 | 7 | 43.8 | 2 | 12.5 | 2 | 12.5 | |
| *Murraya paniculata* | 103 | 17 | 16.5 | 5 | 4.9 | 28 | 27.2 | 53 | 51.5 | 3 |
| *Zanthoxylum dissioides* | 2 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 2 | 100.0 | |
| SAPINDACEAE (207 indv., 4 spp., 4 gen.) | | | | | | | | | | |
| *Amesiodendron chinense* | 57 | 16 | 28.1 | 10 | 17.5 | 2 | 3.5 | 29 | 50.9 | |
| *Delavaya yunnanensis* | 41 | 10 | 24.4 | 13 | 31.7 | 5 | 12.2 | 13 | 31.7 | 56 |
| *Litchi chinensis* | 105 | 60 | 57.1 | 0 | 0.0 | 31 | 29.5 | 14 | 13.3 | |
| *Sapindus mukoross* | 4 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 4 | 100.0 | |
| SIMARUBACEAE (10 indv., 2 spp., 2 gen.) | | | | | | | | | | |
| *Brucea mollis var. tonkinensis* | 8 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 8 | 100.0 | |
| *Picrasma quassioides* | 3 | 0 | 0.0 | 0 | 0.0 | 1 | 33.3 | 2 | 66.7 | |
| SOLANACEAE (159 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Solanum verbascifolium* | 159 | 0 | 0.0 | 44 | 27.7 | 55 | 34.6 | 60 | 37.7 | |
| STERCULIACEAE (643 indv., 4 spp., 2 gen.) | | | | | | | | | | |
| *Pterospermum heterophyllum* | 74 | 33 | 44.6 | 1 | 1.4 | 9 | 12.2 | 31 | 41.9 | |
| *Sterculia euosma* | 558 | 63 | 11.3 | 7 | 1.3 | 173 | 31.0 | 315 | 56.5 | 41* |
| *S. lanceolata* | 16 | 0 | 0 | 0 | 0.0 | 0 | 0.0 | 16 | 100.0 | |
| *S. nobilis* | 39 | 0 | 0 | 0 | 0.0 | 2 | 5.1 | 37 | 94.9 | |
| STYRACACEAE (1 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| *Styrax suberifolia* | 1 | 0 | 0 | 0 | 0.0 | 1 | 100.0 | 0 | 0.0 | |

Table 2-3 (continued-4)

| Family/Species | Total | Habitat Classse | | | | | | | | Code |
|---|---|---|---|---|---|---|---|---|---|---|
| | | I | | II | | III | | IV | | |
| THEACEAE (2 indv., 1 sp., 1 gen.) | | | | | | | | | | |
| Camellia longgangensis | 2 | 0 | 0 | 0 | 0.0 | 2 | 100.0 | 0 | 0.0 | |
| TILIACEAE (255 indv., 3 spp., 3 gen.) | | | | | | | | | | |
| *Burretiodendron esquirolii* | 4 | 0 | 0 | 0 | 0.0 | 0 | 0.0 | 4 | 100.0 | |
| *Grewia biloba* | 246 | 1 | 0.4 | 2 | 0.8 | 110 | 44.7 | 133 | 54.1 | |
| *Microcos paniculata* | 5 | 0 | 0 | 0 | 0.0 | 0 | 0.0 | 5 | 100.0 | |
| ULMACEAE (804 indv., 5 spp., 3 gen.) | | | | | | | | | | |
| *Celtis austro-sinensis* | 30 | 5 | 16.7 | 0 | 0.0 | 15 | 50.0 | 10 | 33.3 | 5* |
| *C. philippinensis* | 1 | 0 | 0 | 0 | 0.0 | 0 | 0.0 | 1 | 100.0 | |
| *C. sinensis* | 39 | 5 | 12.8 | 2 | 5.1 | 16 | 41.0 | 16 | 41.0 | 35* |
| *Pteroceltis tatarinowii* | 772 | 14 | 1.8 | 73 | 9.5 | 148 | 19.2 | 537 | 69.6 | 2* |
| *Trema orientalis* | 15 | 0 | 0 | 5 | 33.3 | 10 | 66.7 | 0 | 0.0 | |
| URTICACEAE (115 indv., 2 spp., 1 gen.) | | | | | | | | | | |
| *Debregeasia edulis* | 113 | 8 | 7.1 | 0 | 0.0 | 40 | 35.4 | 65 | 57.5 | 45 |
| *D. longifolia* | 2 | 0 | 0 | 0 | 0.0 | 2 | 100.0 | 0 | 0.0 | |
| VERBENACEAE (285 indv., 6 spp., 4 gen.) | | | | | | | | | | |
| *Callicarpa longissima* | 3 | 0 | 0 | 0 | 0.0 | 0 | 0.0 | 3 | 100.0 | |
| *C. macrophylla* | 9 | 0 | 0 | 0 | 0.0 | 2 | 22.2 | 7 | 77.8 | |
| *Clerodendron fragrans* | 112 | 0 | 0 | 3 | 2.7 | 104 | 92.9 | 5 | 4.5 | |
| *Premna fulva* | 26 | 0 | 0 | 6 | 23.1 | 5 | 19.2 | 15 | 57.7 | |
| *Vitex negundo* | 7 | 0 | 0 | 0 | 0.0 | 0 | 0.0 | 7 | 100.0 | |
| *V. quinata* | 130 | 14 | 10.8 | 10 | 7.7 | 58 | 44.6 | 48 | 36.9 | 57 |

**Table 2- 4 Species richness along transects in the 24 units**

| Units | Transects | SL1) | TL2) | Indv3) | Species | Genera | Families |
|---|---|---|---|---|---|---|---|
| LB (IV) | 9 | 10 | 330 | 346 | 41 | 39 | 22 |
| LG (IV) | 20 | 4 | 581 | 488 | 58 | 54 | 29 |
| LGQ (III) | 27 | 4 | 1122 | 1510 | 66 | 53 | 32 |
| LGS1 (IV) | 7 | 8 | 232 | 217 | 25 | 22 | 16 |
| LGS2 (IV) | 8 | 20 | 281 | 307 | 30 | 29 | 20 |
| LGS3 (IV) | 9 | 20 | 382 | 425 | 48 | 41 | 25 |
| LGS4 (IV) | 9 | 10 | 327 | 417 | 60 | 52 | 30 |
| LGT (I) | 5 | 50 | 250 | 292 | 28 | 24 | 19 |
| LH (IV) | 27 | 6 | 989 | 862 | 60 | 53 | 30 |
| LL (IV) | 50 | 5 | 1888 | 1899 | 84 | 66 | 32 |
| LLGQ (III) | 4 | 30 | 170 | 209 | 28 | 25 | 20 |
| LLI1 (I) | 5 | 20 | 220 | 226 | 30 | 28 | 18 |
| LLI2 (III) | 3 | 25 | 125 | 157 | 24 | 21 | 17 |
| LLI3 (III) | 12 | 4 | 468 | 646 | 53 | 45 | 28 |
| LLI4 (I) | 5 | 40 | 240 | 717 | 23 | 21 | 14 |
| LLN (III) | 16 | 15 | 613 | 647 | 54 | 50 | 25 |
| LN (III) | 27 | 5 | 869 | 921 | 58 | 52 | 27 |
| LW (II) | 10 | 20 | 425 | 462 | 41 | 36 | 23 |
| LWG (IV) | 27 | 6 | 875 | 764 | 76 | 63 | 31 |
| LYE (I) | 3 | 50 | 150 | 211 | 33 | 27 | 18 |
| LYG (III) | 7 | 5 | 178 | 299 | 43 | 39 | 26 |
| LY1 (II) | 7 | 20 | 275 | 282 | 40 | 34 | 20 |
| LY2 (II) | 11 | 6 | 436 | 567 | 45 | 40 | 27 |
| LY3 (I) | 3 | 50 | 150 | 158 | 21 | 19 | 13 |

1) SL= shortest length of transects (m). 2) TL= total length of transects. 3) Indv = individual plants

habitat types were more likely to occur in less disturbed areas, diversity of plant species should increase with habitat quality, which was supported by a significant correlation between ratio 1 (the Shannon-Weaver Index / area surveyed) and habitat quality (Spearman rank correlation $r_S = 0.347$, $n = 24$, one-tailed, $p < 0.05$). Species evenness is demonstrated in *Figure 2- 9*. Species evenness in habitat Class I varied more drastically than that in other habitat classes, which varied around 0.8 (mean = 0.8337, n=24). The first plot was LLI1, a valley that had never been converted to agricultural use due to the narrow flat land with numerous rocks and the difficult access across the ridge between LGS4 and LLI1. Thus plant species requiring rare microhabitat types were found in the valley, which increased diversity. The second plot was LLI4, a valley that was seasonally flooded every year. The water could be as deep as 2.5 – 3m. Such habitat was especially suitable to those species tolerating water such as *Lindera* spp. A total of 712 plants were encountered in LLI4, of which 435 were the individuals of *Lindera pulcherrima.* These individuals accounted for 61.1% of plants sampled in this valley and 86.3% of the individuals of this species in the main study area (see Appendix A), indicating a clumped distribution of this plant species in the valley.

There were 19 common families, in each of which the number of individuals accounted for over 1.6% of the total number of plants, and the plants of the 19 families accounted for 89.9% overall (see *Table 2- 6*). It is shown that even the common family members were more likely found in better habitat.

There were 6 families in which there were more than five species, including the Caesalpiniaceae (10 species, accounting for 6.1% of the total number of species), Euphorbiaceae (21 species, 12.8%), Moraceae (16 species, 9.8%), Papilionaceae (10 species, 6.1%), Rutaceae (6 species, 3.6%), and Verbenaceae (6 species, 3.6%) (*Table 2- 3*). They accounted for 42% of the total number of species. There were 20 common species which accounted for 65.5% of the total individuals, while these species made up only 12.1% of the total number of species (see *Table 2- 6*). Generally speaking, these species were distributed more in Habitat Class II than in other habitat classes.

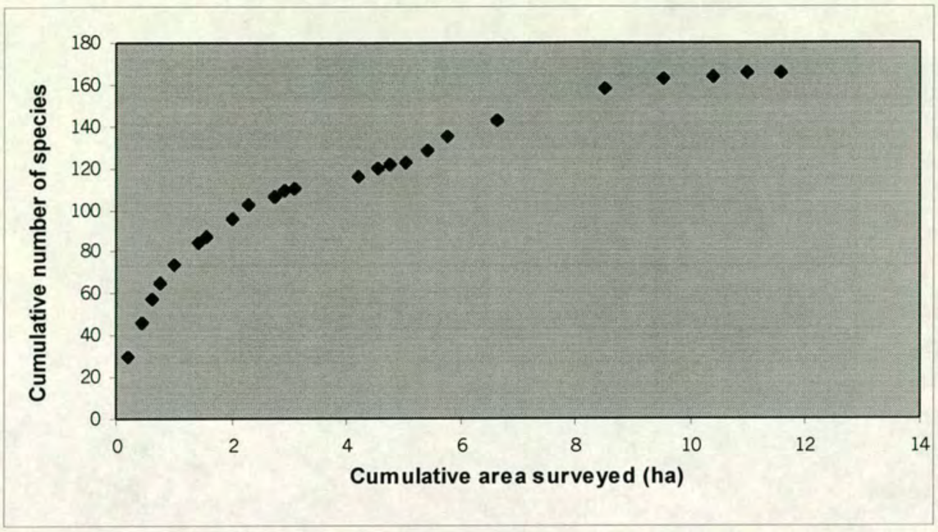


Figure 2- 8 Relationship between area surveyed and number of plant species.

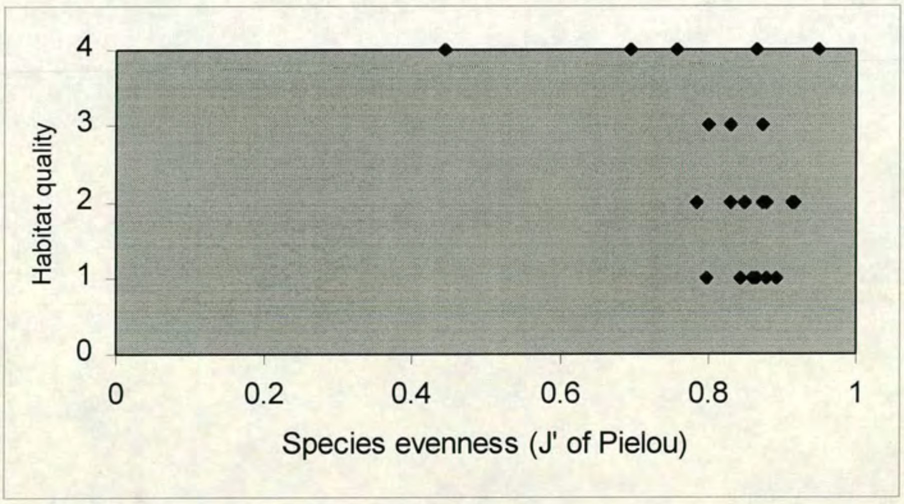


Figure 2- 9 Species evenness in each unit. (For details of habitat quality, see Table 2-1)

**Table 2- 5 Species diversity in each unit (measured with the Shannon-Weaver and Simpson Indices)**

| | LLI1 (1) | LLI4 (2) | LYE (3) | LY3 (4) | LGT (5) | LW (6) | LLI2 (7) | LLI3 (8) | LY1 (9) | LY2 (10) | LYG (11) | LLGQ (12) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Shannon | 3.229 | 1.396 | 3.023 | 2.120 | 2.522 | 3.088 | 2.779 | 3.486 | 3.226 | 3.045 | 3.444 | 3.042 |
| Simpson | 21.460 | 2.388 | 14.573 | 3.950 | 8.068 | 15.187 | 11.364 | 24.959 | 16.927 | 13.360 | 24.868 | 16.415 |
| area (ha) | 0.22 | 0.24 | 0.15 | 0.15 | 0.25 | 0.42 | 0.12 | 0.47 | 0.28 | 0.44 | 0.18 | 0.17 |
| Ratio 1 | 14.677 | 5.817 | 20.155 | 14.133 | 10.087 | 7.352 | 23.158 | 7.417 | 11.523 | 6.921 | 19.131 | 17.894 |
| Ratio 2 | 97.548 | 9.948 | 97.155 | 26.333 | 32.272 | 36.160 | 94.702 | 53.104 | 60.454 | 30.364 | 138.157 | 96.560 |

| | LGQ (13) | LB (14) | LGS1 (15) | LGS2 (16) | LGS3 (17) | LGS4 (18) | LWG (19) | LL (20) | LH (21) | LN (22) | LLN (23) | LG (24) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Shannon | 3.479 | 3.213 | 2.876 | 2.945 | 3.400 | 3.598 | 3.721 | 3.739 | 3.272 | 3.185 | 3.389 | 3.501 |
| Simpson | 24.725 | 16.472 | 13.709 | 13.610 | 23.202 | 25.697 | 28.834 | 28.366 | 15.332 | 13.094 | 19.478 | 23.296 |
| area (ha) | 1.12 | 0.33 | 0.23 | 0.28 | 0.38 | 0.33 | 0.88 | 1.89 | 0.99 | 0.87 | 0.61 | 0.58 |
| Ratio 1 | 3.106 | 9.736 | 12.504 | 10.518 | 8.948 | 10.902 | 4.228 | 1.978 | 3.305 | 3.661 | 5.556 | 6.036 |
| Ratio 2 | 22.076 | 49.914 | 59.603 | 48.607 | 61.057 | 77.868 | 32.766 | 15.009 | 15.487 | 15.050 | 31.931 | 40.166 |

Ratio 1 is the Shannon-Weaver Index divided by the area, and Ratio 2 is the Simpson Index divided by the area. Area (ha) was calculated using the data in Table 2-4. It was the surveyed area but not the total area of that unit.

**Table 2- 6 List of the 19 commonest families and the 20 commonest species**

| Families | No. Genera | No. Species (%) | No. Individuals (%) | Species | Family | No. Individuals (%) |
|---|---|---|---|---|---|---|
| ALANGIACEAE | 1 | 1 (0.6) | 527 (4.0) | *Alangium chinense* | ALANGIACEAE | 527 (4.0) |
| ANACARDIACEAE | 3 | 3 (1.8) | 405 (3.1) | *Albizzia kalkora* | MIMOSACEAE | 477 (3.6) |
| ANNONACEAE | 4 | 5 (3.0) | 220 (1.7) | *Alchornea rugosa* | EUPHORBIACEAE | 225 (1.7) |
| BIGNONIACEAE | 3 | 3 (1.8) | 842 (6.4) | *Broussonetia papyrifera* | MORACEAE | 211 (1.6) |
| CAESALPINIACEAE | 3 | 10 (6.1) | 204 (1.5) | *Cipadessa cinerascens* | MELIACEAE | 640 (4.8) |
| EUPHORBIACEAE | 13 | 21 (12.8) | 2405 (18.2) | *Clausena excavata* | RUTACEAE | 277 (2.1) |
| LAURACEAE | 2 | 4 (2.4) | 1429 (10.8) | *Croton kwangsiensis* | EUPHORBIACEAE | 212 (1.6) |
| MELIACEAE | 4 | 5 (3.0) | 645 (4.9) | *Cudrania cochinchinensis* | MORACEAE | 398 (3.0) |
| MIMOSACEAE | 4 | 5 (3.0) | 557 (4.2) | *Desmos cochinchinensis* | ANNONACEAE | 202 (1.5) |
| MORACEAE | 4 | 16 (9.8) | 1318 (10.0) | *Fluggea virosa* | EUPHORBIACEAE | 594 (4.5) |
| MYRSINACEAE | 3 | 4 (2.4) | 211 (1.6) | *Grewia biloba* | TILIACEAE | 346 (2.6) |
| MYRTACEAE | 2 | 2 (1.2) | 262 (2.0) | *Lindera communis* | LAURACEAE | 418 (3.2) |
| PAPILIONACEAE | 5 | 10 (6.1) | 252 (1.9) | *L. pulcherrima var. attenuata* | LAURACEAE | 504 (3.8) |
| RUTACEAE | 4 | 6 (3.7) | 304 (2.3) | *Litsea euosma* | LAURACEAE | 443 (3.4) |
| SAPINDACEAE | 4 | 4 (2.4) | 207 (1.6) | *Mollotus apelta var. kwangsiensis* | EUPHORBIACEAE | 404 (3.0) |
| STERCULIACEAE | 2 | 4 (2.4) | 687 (5.2) | *M. philippinensis* | EUPHORBIACEAE | 487 (3.7) |
| TILIACEAE | 3 | 3 (1.8) | 255 (1.9) | *Oroxylun indicum* | BIGNONIACEAE | 783 (5.9) |
| ULMACEAE | 3 | 5 (3.0) | 857 (6.5) | *Pteroceltis tatarinowii* | ULMACEAE | 772 (5.8) |
| VERBENACEAE | 4 | 6 (3.7) | 287 (2.2) | *Rhus chinensis* | ANACARDIACEAE | 307 (2.3) |
| | | | | *Sterculia euosma* | STERCULIACEAE | 558 (4.2) |
| TOTAL | 71 | 117 (71.3) | 11874 (89.9) | | | 8685 (65.8) |

Among the top 15 food plant species (detailed in Chapter V), only three species fell into the common species list: *Lindera communis* (Lauraceae), *Pteroceltis tatarinowii* (Ulmaceae), and *Sterculia euosma* (Sterculiaceae). Most food plant species were uncommon, including a species (*Madhuca pasquieri*) whose family (Sapotaceae) was not encountered during the vegetation sampling. *Cuscuta chinensis* (Family Convolvulaceae) was a parasitic vine and was not recorded during sampling. *Table 2- 7* shows the number of individuals of these species encountered in the survey in the main study area. It is shown that these species were more likely to occur in better habitat (Habitat Classes I and II) and their clumped distributions were significantly different from random (Index of Dispersion, $p<0.001$, see *Table 2- 7*).

#### *2.3.2.3 Habitat quality and species richness*

A modest relationship was found between diversity and size of area surveyed (Spearman Rank $r_S = 0.6289$, $n = 24$, $p<0.01$, between area and the Shannon-Weaver Index; and $r_S = 0.4533$, $n = 24$, $p<0.05$, between area and Simpson's Index, both two-tailed). Because of this, data on diversity were divided by the size of units to give a ratio (Ratio 1 was the Shannon-Weaver Index divided by the area and Ratio 2 the Simpson Index divided by the area, see *Table 2- 5*) for a comparison of plant species diversity between units. Ratio 1 was plotted against the extent of human disturbance of the habitat in *Figure 2- 10*. A general trend was shown that plant species diversity decreased with the extent of human disturbance, although the trend was not statistically significant (Spearman Rank $r_S = 0.339$, two-tailed, $p > 0.05$). In other words, plant species diversity tended to increase with habitat quality.

### 2.3.3 Phenology of food plant species

A total of 411 individual food plants, of 43 species, were monitored. Ten individuals were tagged from 40 of these species, 7 individuals from 1 (Spp. 11), and 2 individuals each from 2 species (Spp. 43 & 47), because no more individuals were found in the study area. Of the 38 species that had been tagged before March 1998,

**Table 2- 7 Habitat preference of the top 15 food plant species for the habitat classes in the main study area**

| Species | Family | No. Individuals | Habitat Class* | |
|---|---|---|---|---|
| | | | Class IV | Other classes |
| *Broussonetia kazinoki* | MORACEAE | 4 | 2 | 0 |
| *Capparis viminea* | CAPPARIDACEAE | 13 | 1.08 | 5.44 |
| *Celtis austro-sinensis* | ULMACEAE | 30 | 0.67 | 1.63 |
| *C. sinensis* | ULMACEAE | 39 | 0.82 | 1.34 |
| *Cuscuta chinensis* | CONVOLVULACEAE | ** | | |
| *Ficus microcarpa* | MORACEAE | 12 | 0.34 | 2 |
| *Lindera communis* | LAURACEAE | 418 | 0.34 | 1.66 |
| *Madhuca pasquieri* | SAPOTACEAE | ** | | |
| *Mappianthus iodoides* | ICACINACEAE | 6 | 1.34 | 3.92 |
| *Millettia pachycarpa* | PAPILIONACEAE | 140 | 0.33 | 1.98 |
| *Pithecellobium clypearia* | MIMOSACEAE | 50 | 1.84 | 0.73 |
| *Pteroceltis tatarinowii* | ULMACEAE | 772 | 1.39 | 0.69 |
| *Pueraria thunbergiana* | PAPILIONACEAE | 7 | 2 | 0 |
| *Sterculia euosma* | STERCULIACEAE | 558 | 1.13 | 1.08 |
| *Tetraceae asiatica* | DILLENIACEAE | 6 | | |
| OVERALL | | 2055 | 0 | 3.26 |
| Mean | | | 1.02 | 2.16 |
| Standard error | | | 0.19 | 0.44 |

* For classification of habitat class, see text and Table 2-1. Data in the two columns under this heading are the figures of habitat preference index. This index was calculated using the percentage of individuals of the species divided by the percentage of the area of the habitat class(es). ** Data were not obtained for the two species. For details, see the text.

10 species (26.3%) were deciduous and 15 (39.5%) semi-deciduous. Only 13 species (34.2%) were evergreen. It is thus assumed that the forest was semi-deciduous forest, which is also supported by seasonal variation of leaf cover shown in *Figure 2- 11*. Flowers and fruits occurred at a low level year round and fluctuated seasonally (see also *Figure 2- 12*).

Leaves predominated at all times (see *Figure 2- 11*); they also accounted for most feeding records and supported langurs in the critical season (Chapter V). Fluctuations in availability of young and mature leaves are compared in *Figure 2- 13*. Temperature and rainfall (*Figure 2- 6*) influenced the phenological pattern of plants (Spearman Rank $r_S = 0.7857$ between overall availability of leaves and monthly rainfall, and $r_S = 0.7692$ between overall availability of leaves and mean temperature, $n = 13$, two-tailed, $p<0.01$). However, only rainfall played an important role in the production of fruits (Spearman Rank $r_S = 0.7308$, $n = 13$, two-tailed, $p< 0.05$).

## 2.4 Discussion

### 2.4.1. Habitat type and species diversity in Bapen Reserve

Tree felling makes habitat open, which causes shade-tolerant species and species that require rare habitat types within forest to die out. Perhaps through this mechanism, plant species diversity decreased with the extent of human disturbance (*i.e.*, increased with habitat quality). Common species and families (*Table 2- 6*) were more likely to occur in better habitat (Classes I and II), which may be the outcome of vegetation clearance. That is, vegetation clearance removed both rare and common forms in lower quality habitat (Classes III and IV).

The most important foods of white-headed langurs were rare species (*Table 2- 7*) and were more likely to occur in better habitat (Classes I and II). This may be the reason why langur groups competed for central habitat and did not produce offspring in lower quality habitat (Class IV) (detailed in Chapter V).

### 2.4.2 Climate and phenology

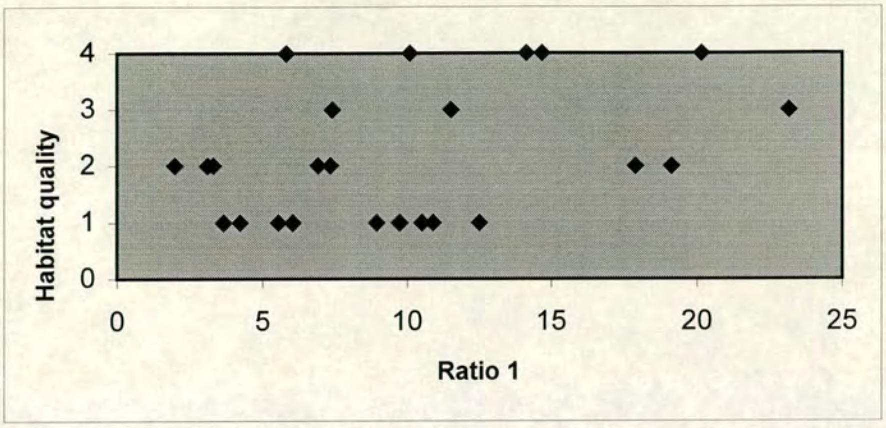


**Figure 2- 10 Correlation between habitat types and plant species diversity**

Plant species diversity is represented by a ratio of the Shannon-Weaver Index/area of each unit.

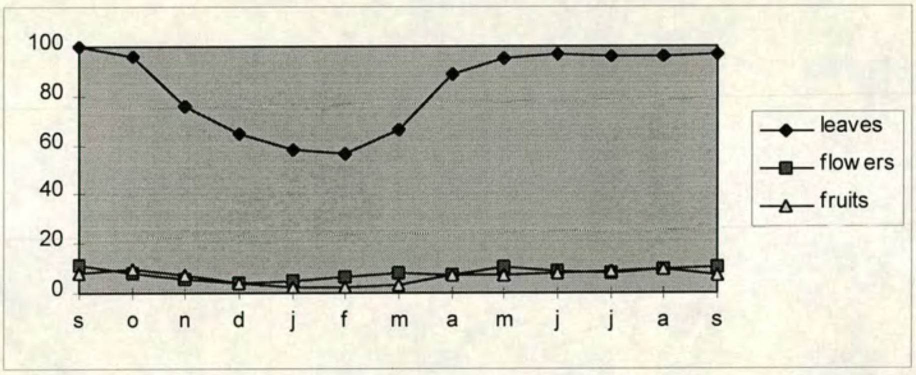


**Figure 2- 11 Fluctuations of leaves, flowers, and fruits.**

Each curve represents the sum of scores of the sub-categories. X-axis: months from Sept. 1997 to Sept. 1998; Y-axis: food availability (actual phenological score / theoretical maximum score x 100%).

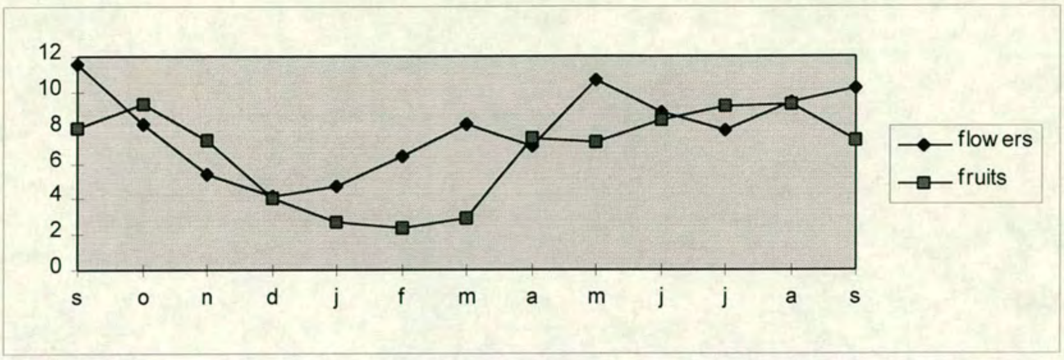


Figure 2- 12 Seasonal fluctuations of flowers and fruits. (Reference to Figure 2- 11)

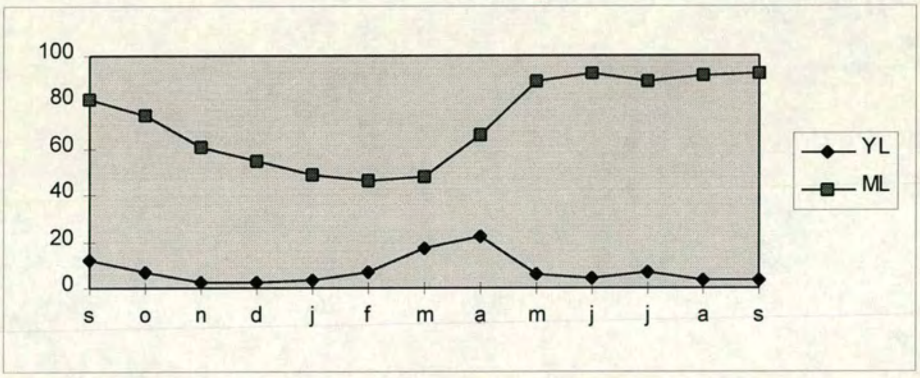


Figure 2- 13 Fluctuations in availability of young and mature leaves. (Reference to Figure 2- 11)

There was a strong correlation between rainfall and the production of fruits in Bapen Reserve. A similar pattern was reported for fleshy fruits in dry tropical forest by Lieberman (1982) in Ghana, but the dry fruited species ripened in the dry season. In Ivory Coast, fruit production is related to a 3-month lag in the time of rainfall (Alexandre, 1980). On Tiwai Island, peak fruiting is in the dry season, but most fruits are dehiscent (cited from White, 1992). Wind dispersed species often fruit in seasons with high winds (Foster, 1982; Terborgh, 1983). In the Lopé Reserve, Gabon (White, 1992; Ham, 1994), a simple correlation is not seen between production of fruits and rainfall. Therefore, it seems that multiple factors are involved in shaping the fruiting pattern in an area, including those of climate.

### 2.4.3 Comparison with other sites

Colobine study sites in Asia in general receive more rainfall than in Africa (Oates, 1994). Simla in India (see *Figure 1- 1*) receives an annual rainfall of 1700mm (Sugiyama, 1976), Kanha in the Indian central highlands 1600mm (Newton, 1988), Kakachi at the southern tip of India 3080mm (Oates *et al.*, 1980). In Sri Lanka, Polonnaruwa receives an annual rainfall of 1670mm (Bennett & Davies, 1994). The annual rainfall is 2000mm in Kuala Lompat, Malaysia, and 3000mm in Sepilok, Indonesia (Raemaekers *et al.*, 1980). Compared to these other colobine study sites in Asia, Bapen Reserve in South China is the driest, with an annual rainfall of about 1168mm during the present study. As at other study sites, the rainfall in Bapen Reserve was seasonal, with a dry season between November and February (*Figure 2-6*). The dry season occurred at a similar time to that in Simla but lasted for longer (see Figure 5.2 of Bennett & Davies, 1994). It is between May and August in Polonnaruwa. The rainfall decreases in February in Kuala Lompat and in April in Sepilok, but there is no true dry season at these two sites. This comparison shows that the dry season in Bapen is the longest among colobine study sites in Asia.

Temperature fluctuates remarkably in Simla between about 10 and 40°C; whereas in Polonnaruwa, Kuala Lompat, and Sepilok, it keeps stable, between 25 and 30°C year round (see Figure 5.2 of Bennett & Davies, 1994). In Bapen Reserve, it ranged from 5 to 38°C during the observation period of the present study (see *Figure 2- 6*a). This range is the widest among all these study sites.

Rainfall seems to have caused a difference in plant species richness between Africa and Asia (Richards, 1952). There are about twice as many tree species in a 1-ha patch at Kuala Lompat or Sepilok as in the evergreen forests of West Africa, *e.g.*, Tai National Park in Côte d'Ivoire and Gola in Sierra Leone (Davies, 1987). It may also be a factor causing differences in plant species richness among Asian colobine sites. In Polonnaruwa and Kanha, there are respectively only 61 species over 5m tall and 63 species > 2m tall (Dittus, 1977; Newton, 1988), the size of which is similar to that of trees in Bapen Reserve. There is a single species dominating the flora: *Drypetes sepiara* in Polonnaruwa and *Shorea robusta* in Kanha. However, in Kuala Lompat, there are 159 tree species (Raemaekers *et al.*, 1980; Bennett, 1983) and in Sepilok over 140 tree species > 10cm dbh in a 1-ha forest patch (see Figure 5.4 of Bennett & Davies, 1994). In Bapen Reserve, there were only about 70 tree and woody liana species ≥ 1.2cm dbh in a 1-ha survey area (*Figure 2- 8*). This species richness is similar to that in Polonnaruwa and Kanha, which seems to be consistent with the fact that these three sites receive the least rainfall. Unlike these two sites is that there was no single species or family dominating the flora in Bapen Reserve (*Table 2- 5*).

Due to the seasonality in climate at these sites, the phenology of vegetation also changes with seasons, but the timing and the amplitude of fluctuations are different between sites. Between April and May in Kanha, young leaves reach their maximum, more than 90% of sampled trees producing young leaves (see Figure 5.5 of Bennett & Davies, 1994). The fluctuation range is between about 15% and 95%. During the same period, fruits are available from only 40% of tree species and flowers from less than 40% of species. In other seasons, fruits maintain a relatively higher level between 20% and 30%. In Kuala Lompat, young leaves fluctuate in a smaller range from less than 5% to about 25%, with a lean season between July and August. Flowers reach 20% in March and fruits about 15% in July. In other months, they maintain a low level between 0 and 5%. In Sepilok, young leaves peak respectively in July and October when they are available from around 50% of sampled tree species. During the lean seasons (in August and from December to February), young leaves are still available from around 10% of sampled species. Flowers and fruits peak respectively in April and July, available from about 10% of sampled trees; but they maintain a level around 1% in other months. In Bapen Reserve, young leaves fluctuated between 2.6 and 21.9% (in April), with a mean of 7.4% (*Figure 2- 13*). In contrast, mature leaves maintained a high level between 46.2 (in February) and 91.9% year round, with a mean of 71.6%. Fruits fluctuated between 2.4 and 9.3% (July and August), with a mean of 6.6%, which was similar to young leaves. These data show that young leaves are less available in Bapen than in Kanha, Kuala Lompat, and Sepilok.

### 2.5 Summary

1. Bapen was in a relatively dry environment where rainfall changed seasonally and temperature fluctuated more widely compared to other colobine study sites in Asia.
2. Species richness was low in Bapen Reserve, which may be caused by the rainfall that was the lowest, compared to other colobine study sites in Asia. Because of human disturbance, plant species diversity decreased with the extent of human disturbance within the Reserve (*i.e.,* increased with habitat quality), and even some common plant forms were largely found only in the valleys with less human disturbance. Rare plant species favoured by white-headed langurs were more likely to occur in areas of higher quality.
3. Vegetation experienced a seasonal change in young leaf flushing and fruiting. Temperature and rainfall have made a significant contribution to shaping leaf phenological pattern and the production of fruits. Data shows that young leaves are less available in Bapen than in other colobine study sites in India, Malay Peninsula, and Borneo.

Chapter III

# LANGUR POPULATION DENSITY

## 3.1 Introduction

Populations of non-human primates are endangered all over the world due to hunting and habitat loss (Strier, 2000). Habitat loss is caused by vegetation clearance and habitat disturbance. The effects of habitat disturbance on primates have been examined for various different primate species. Ganzhorn & Schmid (1998) found that the survival rate of mouse lemurs (*Microcebus murinus*) in primary forest in Madagascar was higher than that in secondary forest, and that the females chose to live in the primary forest. Logging activities in the Way Kambas National Park in Indonesia influenced primate species populations to different extents (Yanuar & Sugardjito, 1993). The most affected species was the agile gibbon (*Hylobates agilis*), while the least affected were the long-tailed macaque (*Macaca fascicularis*) and the silvered langur (*Presbytis cristatus*), whereas the banded leaf-monkey (*P. melalophos*) was affected moderately. Social groups of the Hanuman langur, *P. entellus*, a species very common in India, also avoided disturbed habitat in Sariska Tiger Reserve (Ross & Srivastava, 1994). On Tiwai Island, primates in abandoned farms had a highly frugivorous diet; but other studies on primates in disturbed habitats have suggested that the amount of fruits in the diet is negatively correlated with the use of selectively logged forest and other disturbed habitats (Fimbel, 1994; Johns & Skorupa, 1987). This indicates the response may be site or disturbance specific.

Factors affecting species richness in fragmented habitat are often of interest to conservation programmes. Since the early work done on it (see Chapter III of Soulé, 1986), habitat fragmentation has attracted attention from a few primatologists (Rylands & Keuroghlian, 1988; Schwarzkopf & Rylands, 1989; Ferrari & Diego, 1995). In Central Amazonia, six primate species (*Saguinus midas, Pithecia pithecia, Cebus apetta, Chiropotes satanas, Alouatta seniculus* and *Ateles paniscus*) disappeared from a 10-ha area soon after the area was isolated from its main forest (Rylands & Keuroghlian, 1988). Of these species, *S. midas, P. pithecia*, and *A. seniculus* showed preferences for different forest structures, and thus occurred in different forest fragments (Schwarzkopf & Rylands, 1989).

According to the theory of island biogeography (MacArthur & Wilson, 1967), species richness in an area is proportional to its size. Currently, it is often difficult to conserve large areas of continuous undisturbed habitat because of the increasing density and encroachment of the human population. It is common that a reserve contains several fragmented habitat patches (see Ferrari & Diego, 1995, for the situation in the Atlantic forest of eastern Minas Gerais, Brazil). Thus, a question is proposed in designing a reserve: can many fragmented habitat patches be as good as a single big habitat patch, given the overall size is the same? Because responses of primates to habitat disturbance are site or disturbance specific, different researchers may have different answers to this question. As has been described in Chapter II, habitat fragmentation is an important conservation issue for white-headed langurs. In the present study, the question is whether white-headed langurs prefer fragmented or continuous habitat patches, a question that is addressed in the current Chapter.

The result of habitat disturbance is a long-term decrease in population size. For example, the Tana River red colobus monkeys (*Colobus badius*) decreased in population size by approximately 80% between 1975 and 1986 due to a change of river course and shifting agricultural practices (Decker, 1994). Apart from this study, little effort has been made to monitor changes of primate populations over time (Johns & Johns, 1995, on New World primates and Butynski & Koster, 1994, on primates in Africa).

White-headed langurs were traditionally hunted for medicinal use. Their total population size decreased from more than 600 in the 1970s (Li & Sun, 1982) to only 400 in the early 1980s (Wu, 1983). Reserves were founded for conserving this species at the beginning of the 1980s (see Chapter II), after which the population recovered to 700 in 1987 (M.C. Wu, *pers. comm.*) However, local governments have been pursuing a high economic growth rate over the past ten years without regard to the poor productivity of the area or the effects on the environment. The local community made a tunnel in 1991 for vehicle access into and out of the main study area in Bapen Reserve. This intensified land use, which in turn caused habitat loss. Slopes at the foot of hills were not suitable for cultivation 10 years ago due to many big rocks, but the cultivated land has reached to the stony hill-foot now (see *Plate 3- 1*). According to villagers (N=3), arable land has increased 10 times in the area since 1979, mostly after 1991. From December 1997 to July 1998, seven new patches of land were cultivated on the slopes in the main study area by removing rocks with dynamite, ranging from 10 m² to 25000 m² in patch size. A total area of 3.77ha was lost. Langurs were not seen to use a hill for 7 months after creation of a patch between this hill and another hill (see also Chapter V). *Figure 3- 1* shows the change in arable land use in the study area (532ha) from 1988 to 1998, during which, 347ha (65.2% of the whole area) became used year-round, 115ha (62.0% of the natural habitat) was lost to seasonal use. Only 13.3% had not been used or had been abandoned back to langurs.

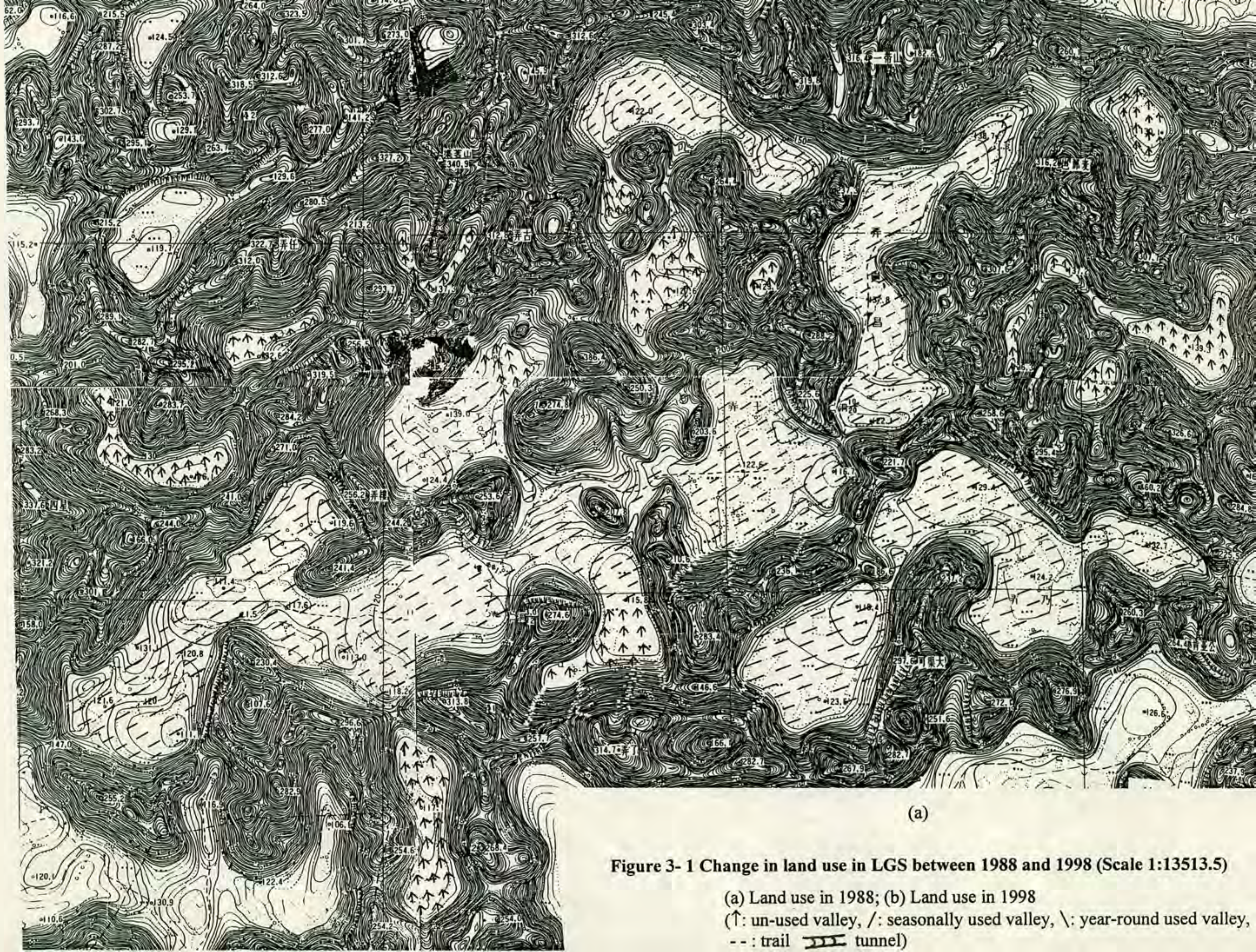
Due to long-term under-funding, the reserve stations have switched their attention from conservation management to seeking for financial resources, which is further encouraged by the government. Consequently, poaching has become common again. In such a situation, the second question to be addressed in this chapter is how has the langur population changed in the past few years? Data presented in this chapter were collected from two reserves only, Bapen and Longgang, so the overall population size of the species will not be estimated here. During the later stages of fieldwork for this study, a research group from Beijing University started working in Luobai Reserve, Chongzuo County. So the estimate of overall population size will be estimated in the future after this research group publishes their data.

## 3.2 Study Animals and Methods

### 3.2.1 Study animals

#### *3.2.1.1 Langur morphology*

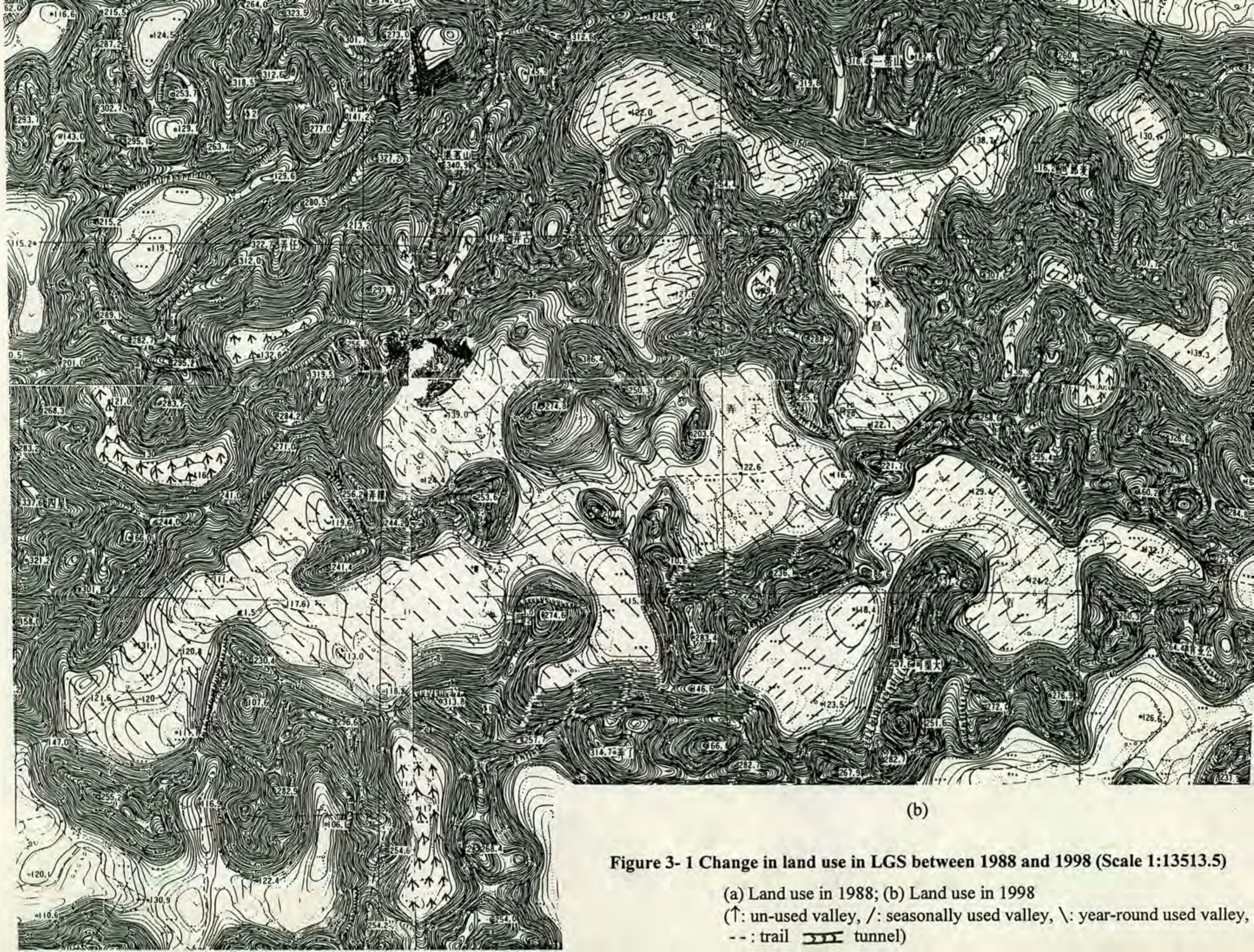
Plate 3-1 A patch of land on hill-foot slope. The vegetation was recently cleared. The rocks would be removed with dynamite. Such a place would often have been the feeding site of langurs.



(a)

**Figure 3- 1 Change in land use in LGS between 1988 and 1998 (Scale 1:13513.5)**

(a) Land use in 1988; (b) Land use in 1998
(↑: un-used valley, /: seasonally used valley, \: year-round used valley,
- - : trail ⫫⫫ tunnel)



(b)

**Figure 3- 1 Change in land use in LGS between 1988 and 1998 (Scale 1:13513.5)**

(a) Land use in 1988; (b) Land use in 1998
(↑: un-used valley, /: seasonally used valley, \: year-round used valley,
- - : trail tunnel)

There is a slight degree of sexual dimorphism in body size. Males are slightly larger than females (Li & Ma, 1980). Pelage from shoulders to head and proximal tail is white. There are also white patches on the dorsal side of the limbs. There are individual differences in the proportion of white on the tail. The intermembral index is 83.04 ([humerus + radius length / femur + tibia length] × 100) (Pan & Peng, 1993). A constant feature used to identify the sexes is that the sexual skin is covered with white hair in females and with black hair in males. Hair in males is brighter than that in females (Li, *pers. obs.*). Hair coloration changes with age. The hair of the new born (in month 1) is reddish brown. The colour changes into bright brown in infants (between month 1 and the end of year 1), becomes lighter and lighter, and is yellow to light grey in juveniles (years 2 and 3), after which black and white patches appear in adults (above 3 years). The basic coloration in adults is black and white. However, the hair becomes dull brown again when langurs are in old age (after 10 years in males and 8 years in females).

#### *3.2.1.2 Ecological habits*

White-headed langurs live in groups on limestone hills. A group is normally composed of an adult male, several adult females, and their offspring (detailed in Chapter VI). Such a bisexual group is usually cohesive and their activities are synchronised. A loud call is used in inter-group communication and to maintain space between groups. When two groups encounter each other, one group moves away so as to keep a minimum distance of about 150m from the other. Any two bisexual groups do not stay on a single hill (*pers. obs.*; see also Lai, 1987). There are two feeding peaks, one in the morning between 0830 and 1000 hrs, the other in the afternoon between 1530 to 1830 hrs (Li, 1993b). These feeding peaks are the most active time, when langurs can be detected from noises made when picking leaves and jumping between trees or tree branches. Because of the sparse distribution of vegetation on hills, they are very easy to observe when active. Langurs often move on cliff ledges and stay in caves overnight. Faeces and urine are left on the rock of cave entrances and ledges. The stains are bright if the site is still used and dull if abandoned sometime earlier, so stains were used as a reliable indirect sign for judging whether there were langurs in the area.

### 3.2.2 Review of field techniques

There are several field techniques that could be used for primate population surveys , including line transect census, nonlinear density plot method, quadrat censuses, fixed-point counts, mark-recapture, and nest counts (SCNP, 1981; Brockelman & Ali, 1987; Rabinowitz, 1993; Sutherland, 1996).

*Mark-recapture* techniques have been used extensively in population studies of small mammals including small primates, such as marmosets and Howler monkeys (Thorington *et al.*, 1979). Researchers make use of the proportion of marked-to-unmarked individuals in a series of catches in order to determine population size and density. However, this technique is not now recommended for studies on primate population density, particularly where arboreal species are involved, because it can be harmful to the animals, time-consuming, and expensive.

*Nest counts*: This method consists of counting nests in a predefined area, usually a transect of known length and fixed width. The total number of nests divided by the area searched gives nest density. This technique is applicable to primates making night nests, *i.e.*, the great apes.

*Fixed-point counts*: In this method the observers remain at a site and record all primate groups seen or heard. It is suggested that this technique useful only to determine relative abundance, but not to extrapolate absolute density.

*Nonlinear density plot method*: When time and resources are limited and information from interview has confirmed that the species of interest is not selectively hunted, researchers conduct a preliminary exploration of the region, making notes of vegetation height and quality and on soils and general topography. During the initial encounters with primates, attempts should be made to estimate group size and the distance from which the group was detected, and to determine what the animals were doing when detected. A few days later, a group is selected and an attempt made to study it through an entire day, recording the number of individuals in the group and estimating the approximate daily range. Data from this work are a useful indicator of relative density. Using existing knowledge about density from other areas, the following procedure is then adopted: each transect length is set, so that for a known detection width it will cover an area equal to half of the average home range of the species. Each transect will then be treated as a single plot. At least ten transects are necessary and placed randomly in the habitat. The real density of groups per unit area is estimated using a Poisson distribution from the percentage frequency of groups per sampling unit or plot. Two requirements must be met: *a)* study animals are not selectively hunted, and *b)* detailed knowledge on population density of the species must be available from other areas.

*Line transect census*: This is a widely used technique. Transects are randomly predetermined and sampled. When animals are encountered, the following sighting data are collected: perpendicular distance (Y), or sighting distance (D) and sighting angle (θ, angle between the direction of the transect line and the line of sight to the animal). D and θ can be measured using a range finder and a compass, and are used to calculate Y. Before sampling, the length of transect lines is known, thus the area surveyed can be calculated. The accuracy of animal group density estimates is a major concern because canopies or natural objects influence detectability, thus transect replicates are needed, the number of which depends on the 95% confidence limits. When the technique is used, the following criteria must be met (Rabinowitz, 1993):

1. Animals and transect lines are located randomly throughout the census area, or "typical" areas are selected based on principal forest types.
2. The habitat is homogeneous (otherwise the transects should be stratified).
3. Animals do not move away before being detected, and the distances are measured to the initial location of the animals.
4. Sighting of one animal or group is independent of sightings of others. Noises or behaviour of sighted animals do not influence the actions of other animals in the area.
5. The animals' response to the observer remains consistent throughout the census.
6. No animal is counted twice during the same transect walk.

It is obvious that these criteria are very difficult to meet. For example, the animals' response to the observer is often variable. Some animals that have been harmed before may move away on seeing the observer. These factors influence the precision of data. In the present study on white-headed langurs, limestone hills are the habitat used, where transect lines could not be located randomly. Only existing paths were accessible. Langurs living in different areas responded differently to the presence of man; some kept silent after seeing the observers, others rushed away quickly (*pers. obs.*).

The objective of the line transect sampling is to estimate population density, thus any factors influencing animal detectability will influence data accuracy. It is obvious that animal detectability decreases with increasing distance from the observer to the animals of interest. So it is necessary to estimate an effective strip width (Brockelman & Ali, 1987; Rabinowitz, 1993). There are five methods for calculating animal density from line transect sampling data (Rabinowitz, 1993). The first is to use average perpendicular distance multiplied by transect length to give a surveyed area which is then used in the calculation of population density. The second is Kelker's method, using path-to-animal distances to establish a frequency histogram, where detection probability falls off. The fall-off point is then used as the effective strip width. The third is King's method, in which the mean sighting distances are used for calculation. The fourth is Webb's method, which uses the mean sighting angle and the mean sighting distance to determine the mean perpendicular distances. The fifth is Hayne's method. This method is based on the premise that the probability of occurrence depends on the distance from the observer, and thus sightings are divided into distance classes. The density formula is the same as King's, but the gradient of detectability is taken into account.

Some authors have proposed in recent years new techniques to deal with problems raised by line transect sampling, such as Lahm *et al.* (1998) and Stoner (1994); but these are statistical techniques for analysing field data collected using the same basic technique.

### 3.2.3 Field procedures

Two types of fieldwork were carried out. One was finite population sampling. It was used to determine the population density of langurs over the whole Bapen Reserve (including hill-groups of GP, LGS, QN, GF, and MZ, see *Figure 2- 3*) from December 1996 to April 1997, and in detail over part of LGS from April to September 1998. The other was a general population survey in Longgang Reserve (LGR, *Figure 2- 4*) between December 1996 and April 1997. In each case, the area surveyed was measured on maps scaled at 1:10,000 or 1:5,000. No account was taken of contours.

*Finite surveys over the whole Bapen Reserve:* Daily work started at 0730 hrs and ended at 1800 hrs. Searching for langurs was conducted during their active time. The hill-groups were surveyed in a sequence from GP, LGS, QN, MZ, to GF. A given hill-group was surveyed section by section. Each section was pre-determined and then surveyed in a working day. A section was a part of a hill-group, the size of which depended on the following factors:

1. Continuity among hills: When hills in the section were mostly interconnected with high ridges, field workers had to either spend a large amount of energy climbing, or walk a long way from one valley to another. This information was available from maps. In this case, the section size was smaller.
2. Number of accessible valleys: In a few cases, valleys were closed by cliffs and there was no trail reaching to these valleys, so they could not be surveyed. In such a case, the section to be surveyed could be large.

Surveys were carried out along existing trails. Researchers paced along trails, stopping every 100m to search hills through binoculars and record information of locality and time when animals were detected, duration of observation, activity when first detected, age-sex composition of groups, and height of the group on the hill. The census routes in each hill-group are shown in *Figure 3- 2* to *Figure 3- 6*.

**Figure 3- 2 Census routes in GP (scale 1:22,727.3)**

- - → : trails used in the fieldwork; ---| : end of census routes; ═ : highway; ▨ : village; number along the routes: sequence of days when the hill-group was surveyed. Hills with the same number (*e.g.*, 1) were surveyed on that day (*e.g.*, day 1). ★: Starting point of a day survey.

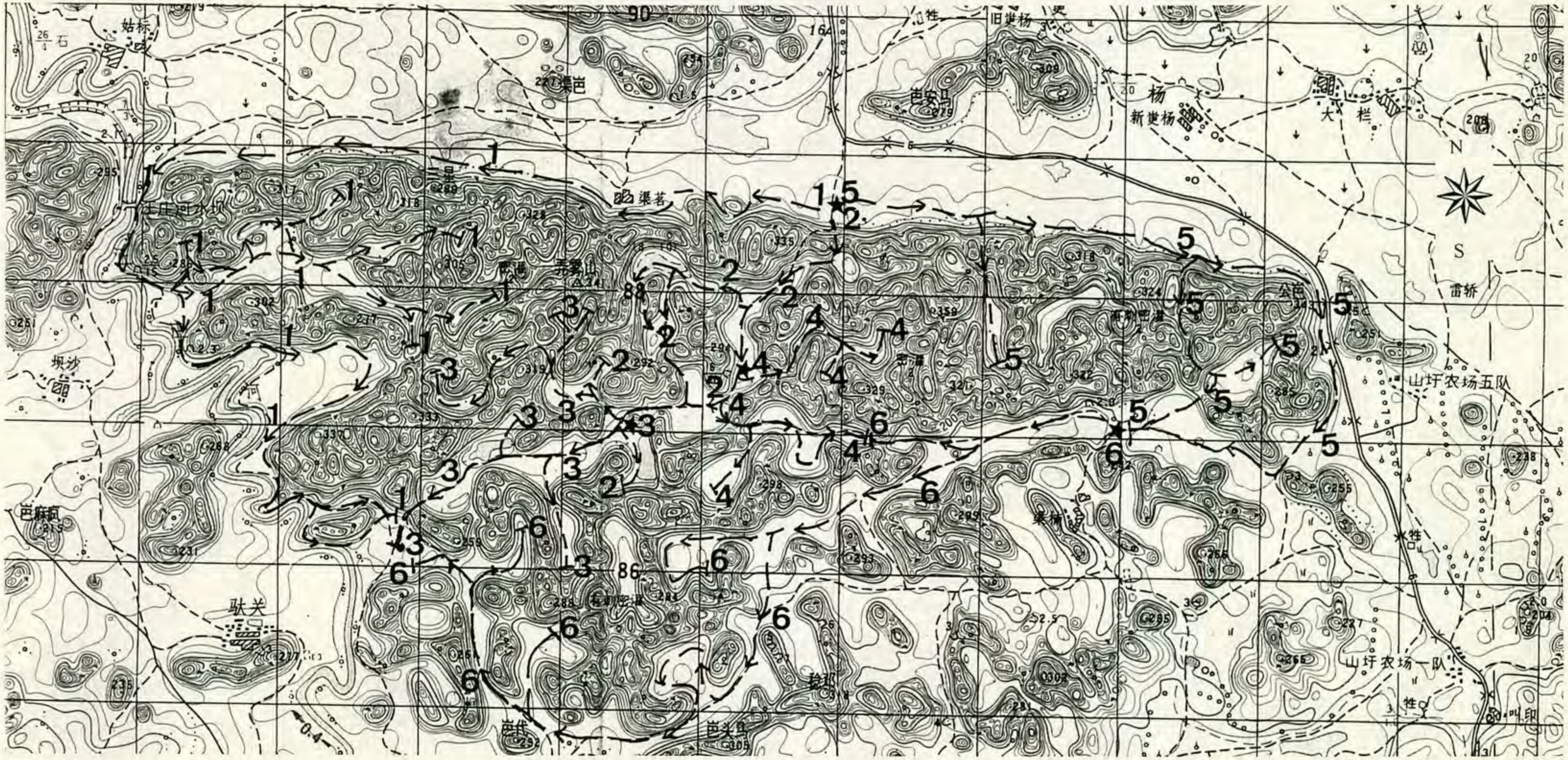


Figure 3- 3 Census routes in LGS (scale 1:40,000)

(for legend, see Figure 3- 2)

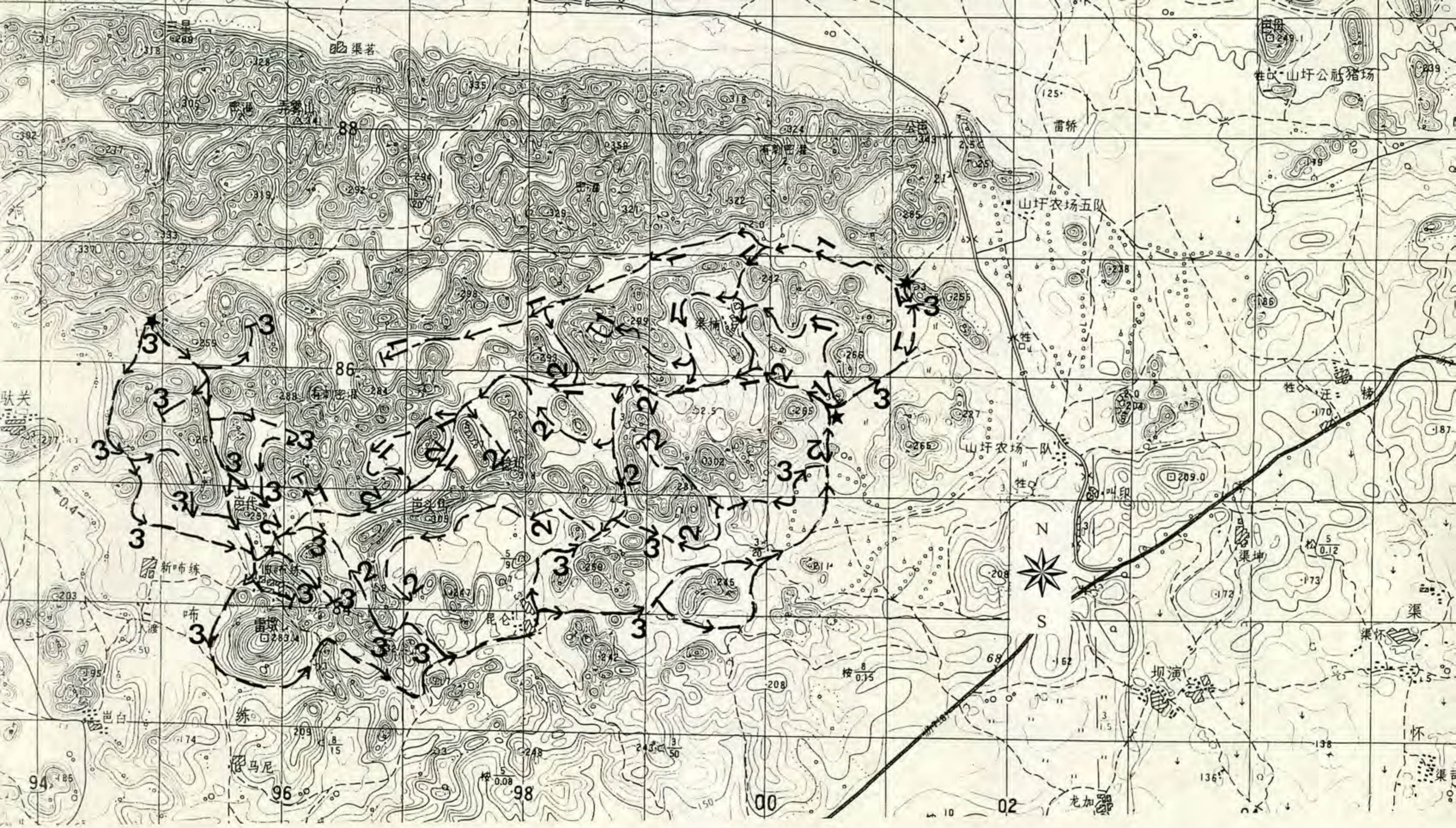


**Figure 3- 4 Census routes in QN (Scale 1:41,666.7)**

(for legend, see Figure 3- 2)

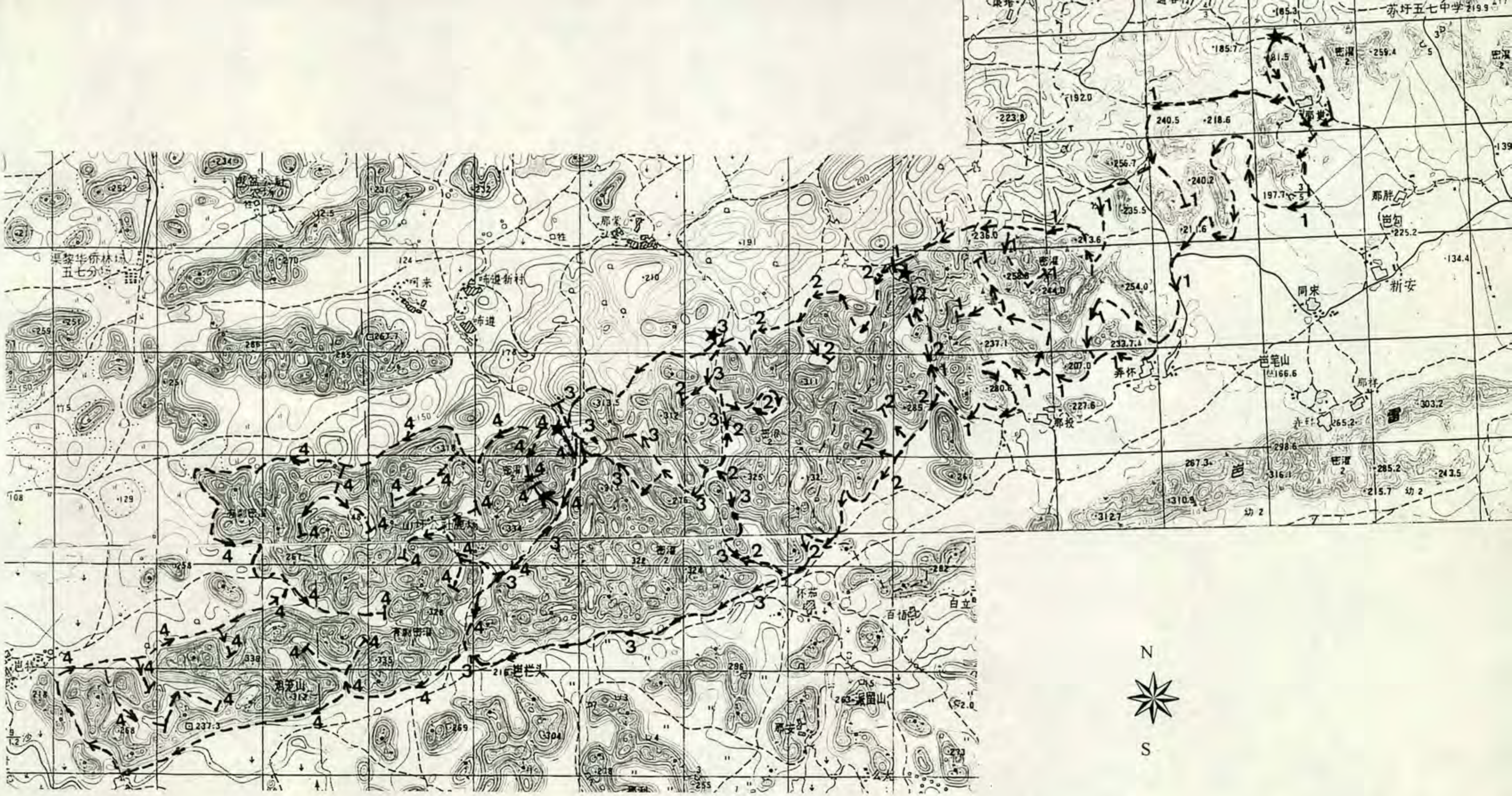


Figure 3- 5 Census routes in MZ (Scale 1:50,000)

(for legend, see Figure 3- 2)

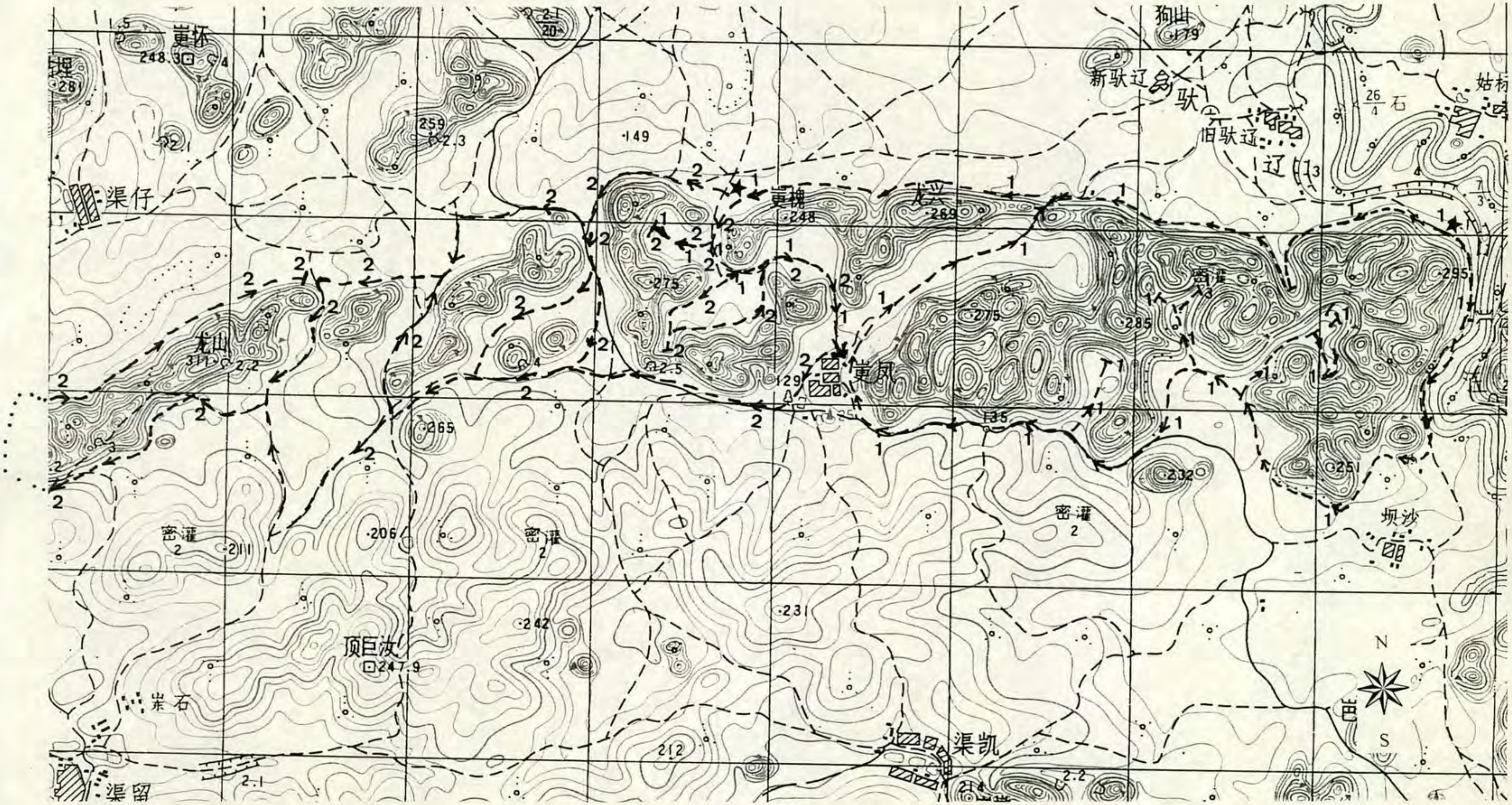


**Figure 3- 6 Census routes in GF (Scale 1:28,571.4)**

(for legend, see Figure 3- 2)

*Detailed censuses over part of Bapen Reserve:* This work was conducted in the main study area in LGS, Bapen Reserve, from March to September 1998. As in the broad survey, existing trails were used in this census due to the tough terrain. This did not meet the requirements that the length of trails should be predetermined and the trails established randomly without bias to terrain, vegetation, and other factors; but it was the only feasible way to survey langur population density in the area. A census was carried out twice per month from March to August and once in September along the following lines:

Line 1*: from LB, through LGS1, LGS2, LGS3, LGS4, LWG, LL, to LH (Figure 2- 5);*
Line 2*: from LG, through LYE, to LGT, and through LY1, LY2, to LY3;*
Line 3*: from LYG, through LLGQ, to LGQ;*
Line 4*: from LLI1, through LLI2 to LLI3 and LLI4; and*
Line 5*: from LN to LLN.*

These lines covered the whole main study area, including all four classes of habitat (see Chapter II). During the census, the researcher stopped every 200-400 m to look and listen, trying to detect any sign of langurs. Searching lasted for 30min, because according to field observation, langurs did not keep still longer than this without any motion. When langurs were found, a maximum of 1 hr was spent for observation, recording information on group composition and the locality; when no langurs were found, the researcher moved to the next site and repeated the procedure.

Survey line width estimation is a crucial aspect of this technique. It is estimated by measuring the perpendicular distance from animals to the trail. In the current research, cliffs at the two sides were searched, thus the survey width was equal to the perpendicular distance from cliff to the survey trail. Langurs were often high on the cliff, which resulted in the distance between langurs and the survey trail being greater than the actual survey width. So an alternative way was to measure the area surveyed on the maps of 1:5,000 in scale.

The following calculations were made to yield estimates of population density:

(1) Standard deviation (s):

$$\mathbf{s = \sqrt{\{\sum X^2 - [(\sum X)^2/n]\}/(n-1)}}$$

where X was the number of groups encountered along each trail, n was the number of trails, and (n-1) the degree of freedom.

(2) 95% confidence limits (cl):

$$\mathbf{cl = t_{0.05(n-1)} \times s/\sqrt{n}}$$

where *t* was the critical values of Student's *t*-distribution obtained from two-tailed *t* table (used when dealing with small samples of fewer than 100).

(3) The % precision:

$$\mathbf{\%\ Precision = (cl\ /\ m) \times 100}$$

where m was the mean of group numbers (X). The lower this percentage, the more precise the estimated mean.

(4) Group density ($D_1$), where **$D_1$ = number of groups sighted / area surveyed**

(5) Population density ($D_2$), where **$D_2 = D_1 \times$ mean group size**

*Survey in Longgang Reserve (LGR):* Researchers paced along trails, stopping every 100m to search for animals. When langurs were detected, the same data were collected again. Information on the length and width of survey along each trail was derived from maps. The transect codes in *Figure 2- 4* represented the number of transects. Each transect line was sampled in a working day, and three replicates were made for each line.

Four factors were involved in identifying langur groups: *distance between localities, possibility of misclassification, animals' activity when detected,* and *duration of* *observation*. Sexual skin was used to identify the sex of adult langurs. Age phases were classified according to pelage coloration.

*(1) Distance between localities*: When langurs were recorded in two localities at the same time and the distance was > 150 m, they were identified as two different groups.

*(2) Activity*: When two records were made at nearly the same time from two localities, and the distance between the localities was < 150 m, their identity was judged according to the langurs' activity. When one group moved toward the other, it was assumed that they belonged to the same group; when they moved apart from each other, they belonged to two groups.

*(3) Duration of observation*: When langurs stayed in trees or on the hilltop, information on group composition was not always accurate if the observation time was short. The field workers normally needed at least 30min for accurate observation. However, this was not always possible because langurs might move away before researchers made a complete record. In such cases, the record was discarded.

*(4) Possibility of misclassification*: When two records were made from the same (or near) area on different days and when group size was the same, they were identified as the same groups if differences occurred only in the neighbouring age phases, such as infant/juvenile or subadult male/adult female. This is because the coloration of some individuals was intermediate between typical infant and juvenile coloration. Also, adult females were similar in size to subadult males and the sexual skin was not always seen with confidence. When group size was different, and the number of adults was also different, they were identified as two groups.

Indirect sign of langur presence (see above) was used in the survey. When no living animals were observed, our attention was switched to fresh signs. When signs were found, we repeated the survey in that hill-group; when there were no signs, we judged that there were no langurs living in the hill-group.

## 3.3 Census Results

There were 209 langurs encountered, 202 living in 27 groups, plus a pair of young males and five solitary old males. Of these 27 langur groups, 19 were encountered in Bapen Reserve and 8 in LGR.

### 3.3.1 Finite survey over the whole Bapen Reserve

Five transect replicates were made along the routes in LGS and MZ, 3 in QN and LG, and one was in GP and GF, covering an area of 97.4km², of which 91% was accessible. *Table 3- 1* shows the details.

**Table 3- 1 Area surveyed in the five hill-groups in Bapen Reserve (km²)**

| Hill-groups | LGS | QN | GF | GP | MZ | Total |
|---|---|---|---|---|---|---|
| Total area | 35.1 | 12.0 | 6.0 | 10.0 | 34.3 | 97.4 |
| Accessible area | 32.0 | 11.8 | 5.5 | 9.0 | 30.7 | 89.0 |
| % of accessible area | 91% | 98% | 92% | 90% | 90% | 91% |

Nineteen langur groups were found in Bapen Reserve (*Table 3- 2*). Of the five hill-groups in Bapen, GP was the only one in which there were no langurs or indirect signs of their presence. Two groups were heard in GF, but the vocalisation was from a distance. Vocalisations of two bird species (Crow Pheasant coucal, *Centropus sinensis,* and Lesser Crow Pheasant, *C. toulou*) sounded very similar to langur calls when they were heard from a distance. Because no fresh signs were found in the hill-group, the two records from GF were questionable and were excluded from further analysis. Thus the total area surveyed in Bapen Reserve was 91.4km². QN was close to LGS (*Figure 2- 3*), but only a solitary male was found in it. *Table 3- 3* shows that LGS contained the main population pool. The mean group size was 6.79 indv./gr. (129/19), group density 0.21 gr./km² (19/91.4), and population density 1.49 indv./ km² (136/91.4, including the male pair and the solitary males).

**Table 3- 2 Langur groups surveyed in Bapen**

| Gr. No. | Adult | Subadult | Juvenile | Infant | Total |
|---|---|---|---|---|---|
| 1 | 4 | 1 | 1 | 2 | 8 |
| 2 | 3 |  | 2 |  | 5 |
| 3 | M=1,F=2 | 3 | 1 |  | 7 |
| 4 | 3 | 1 |  | 2 | 6 |
| 5 | 3 | 3 | 1 | 3 | 10 |
| 6 | M=1,F=2 |  |  | 2 | 5 |
| 7 | M=1,F=4 |  |  | 4 | 9 |
| 8 | 12 | 2 | 1 | 1 | 16 |
| 9 | 1 | 3 | 1 | 1 | 6 |
| 10 | 2 | 1 | 2 |  | 5 |
| 11* | 4 or | 4 |  |  | 4 |
| 12 | 4 | 1 | 1 |  | 6 |
| 13 | 4 |  | 1 |  | 5 |
| 14 | 5 | 2 |  | 1 | 8 |
| 15 | 3 | 1 | 1 |  | 5 |
| 16 | M=1,F=2 |  | 2 or | 2 | 5 |
| 17 | 3 | 1 |  |  | 4 |
| 18 | 7 | 3 |  | 2 | 12 |
| 19 | M=1,F=2 |  |  |  | 3 |
| Total | 71 (or 75) | 26 (or 22) | 12 (or 14) | 20 (or 18) | 129 |

*Note: Some animals were intermediate between two age phases.

**Table 3- 3 Distribution of groups encountered**

| Hill-group | Gr.No. | No. Indv. | Gr. Size | $D_1$ | $D_2$ |
|---|---|---|---|---|---|
| QN | [1] | [1] | x | x | 0.08 |
| LGS | 18[+2] | 123[+2] | 6.83 | 0.51 | 3.56 |
| MZ | 1[+4] | 6[+4] | 6.00 | 0.03 | 0.29 |
| GF | 2(heard) |  |  |  |  |
| GP | 0 | 0 | 0 | 0 | 0 |
| LGR | 8 | 73 | 9.12 | 2.16 | 19.73 |
| Total | 27 | 202[+7] |  |  |  |

*Note: Numbers in the square brackets are the numbers of solitary langurs in QN and MZ and the male pair in LGS. $D_1$ is group density and $D_2$ population density.

### 3.3.2 Detailed census in the main study area in Bapen Reserve

Thirteen replicate transects were carried out along the five routes which covered the whole study area. *Table 3- 4* shows the details. It is seen in the table that the % precision was high in each transect line (ranging from 46.15% to 97.16%), which indicated that sample size of the area in each line was not large enough. Compared to the single lines, the % precision for the overall (the whole study area) was the lowest, indicating that the estimated mean for the whole study area was more precise. This gave an estimate of population density $D_2 = 6.42$ indv./km² and an estimate of population size of 38 ± 15 langurs in the main study area. Compared to the population density obtained from the finite survey over the whole reserve (1.49 indv./km², see above), it was much higher in the main study area, indicating that white-headed langurs in Bapen Reserve had a highly clumped distribution in the central part of LGS. Data on range use from this Reserve showed that white-headed langur groups living in peripheral habitat with low quality had a very large and poorly-defined home range (see Chapter V). These langur groups were attracted by the higher habitat quality in the central area and were encountered in the main study area during the sampling. This caused a higher population density in the central part of LGS.

### 3.3.3 General survey in LGR

Three replicates were sampled along five transects in Longgang Reserve, covering 3.7 km². *Table 3- 5* shows the details. Eight langur groups were encountered in Longgang Reserve, including 73 langur individuals (*Table 3- 6*). The mean group size was 9.12 indv./gr. (73/8), group density 2.16 gr./ km² (8/3.7), and population density 19.71 indv./ km² (73/3.7).

Data on density in Longgang Reserve were obtained from the central area of the hill-group (*Figure 2- 4*). According to the langur distribution pattern in Bapen Reserve, the population density was much higher in the central area than in the peripheral habitat. The central area in LGR was patrolled regularly and no poaching was reported. Also, the vegetation was least disturbed there. All this may attract

**Table 3- 4 Data from line transects in the study area in LGS, Bapen Reserve**

| Census | Number of group encounters | | | | | |
|---|---|---|---|---|---|---|
| | Line 1 | Line 2 | Line 3 | Line 4 | Line 5 | Overall |
| 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 | 1 | 1 | 0 | 0 | 0 | 2 |
| 3 | 2 | 1 | 0 | 0 | 0 | 3 |
| 4 | 0 | 1 | 0 | 1 | 1 | 3 |
| 5 | 2 | 1 | 0 | 1 | 1 | 5 |
| 6 | 2 | 5 | 1 | 0 | 2 | 10 |
| 7 | 1 | 4 | 3 | 1 | 1 | 10 |
| 8 | 1 | 3 | 1 | 1 | 0 | 6 |
| 9 | 1 | 3 | 3 | 0 | 1 | 8 |
| 10 | 0 | 0 | 0 | 1 | 0 | 1 |
| 11 | 1 | 3 | 0 | 0 | 1 | 5 |
| 12 | 4 | 2 | 1 | 1 | 0 | 8 |
| 13 | 1 | 2 | 0 | 1 | 0 | 4 |
| Total | 16 | 26 | 9 | 7 | 7 | 65 |
| Mean | 1.23 | 2.00 | 0.69 | 0.54 | 0.54 | 5.00 |
| Area (km$^2$)* | 2.30 | 0.96 | 0.54 | 0.46 | 0.81 | 5.32 |
| s | 1.0919 | 1.5275 | 1.1094 | 0.5189 | 0.6602 | 3.2660 |
| cl | 0.6598 | 0.9230 | 0.6704 | 0.3136 | 0.3989 | 1.9735 |
| % Precision | 53.64 | 46.15 | 97.16 | 58.07 | 73.88 | 39.47 |
| $D_1$(gr./km$^2$) | 0.53 | 2.08 | 1.28 | 1.17 | 0.67 | 0.94 |
| Mean group size* | | | | | | 7.58 |
| (broad survey mean group size) | | | | | | 6.83 |
| $D_2$(indv./km$^2$)** | | | | | | 6.42 |

* Mean group size is calculated on the basis of data of the 65 group sightings in the whole study area. **$D_2$ is calculated using broad survey mean group size (see Discussion).

**Table 3- 5 Transect data in LGR**

| | Transect 1 | Transect 2 | Transect 3 | Transect 4 | Transect 5 | Total |
|---|---|---|---|---|---|---|
| Mean survey width (km) | 0.2 | 0.21 | 0.22 | 0.13 | 0.14 | |
| Transect length (km) | 5.35 | 3.9 | 2.9 | 3.8 | 4.7 | |
| Area surveyed (km²) | 1.07 | 0.82 | 0.64 | 0.5 | 0.67 | 3.7 |
| Total area (km²) | | | | | | 20.8 |
| % of surveyed area | | | | | | 17.8 |

**Table 3- 6 Langur groups surveyed in LGR**

| Gr. No | Adult* | Subadult | Juvenile | Infant | Total |
|---|---|---|---|---|---|
| 1 | 5 | | | | 5 |
| 2 | 6 | 2 | 1 | 2 | 11 |
| 3 | 4 | | | 1 | 5 |
| 4 | 5 | | | | 5 |
| 5 | 8 | 2 | 2 | 3 | 15 |
| 6 | 6 | | | | 6 |
| 7 | 15 | | | 2 | 17 |
| 8 | 9 | | | | 9 |
| Total | 58 | 4 | 3 | 8 | 73 |

* Note: The langurs' sex was not distinguished due to the poor observability and the time available for the work in LG.

langurs. Based on this, it is assumed that white-headed langurs in LGR might have a distribution pattern similar to that in Bapen Reserve; *i.e.,* the population density in LGR could be much higher in the central area than peripheral area outside the survey area. Therefore, using these data to extrapolate the population size in the whole reserve would give an overestimate that may provide a mislead basis for conservation action. According to L.R. Lu (*pers. comm.*), no langurs were encountered outside the central area in Longgang Reserve during a 3-day survey.

### 3.3.4 Changes in langur populations over time

In comparison with previous studies (Wu, 1983; Lu & Huang, 1993; Li, 1993a), the langur population of Bapen Reserve may have declined over the past ten years ( *Table 3- 7*). Data collected in 1989 and 1990 cannot be compared because of different field techniques, but 1990 data can be compared directly with the 1997 data. The population in LGS, the main population pool of langurs in Bapen (*Table 3- 3*),

Table 3-7 Changes in the white-headed langur population of Bapen Reserve over time.

| Year | In Bapen | | | | In LGS | | | | Source |
|---|---|---|---|---|---|---|---|---|---|
| | N sightings | Group size | D1 | D2 | N sightings | Group size | D1 | D2 | |
| 1987 | 339 | 7.3±3.0 | 0.39 | 3.48 | | | | | MC Wu, unpbl.data |
| 1989 | | | | | 149 | 7.7±3.2 | 0.63 | 4.2 | Li (1993b) |
| 1990 | | | | | 166 | 5.30±0.62 | 0.99 | 8 | Lu & Huang (1993) |
| 1997 | 136 | 6.79 | 0.21 | 1.49 | 125 | 6.58*±0.93 | 0.51 | 3.56 | This study |

D1: Group density; D2: Population density. *This figure is smaller than that in Table 3- 3, because the male pair is included, so as to be comparable with Lu and Huang (1993).

has changed in three parameters: the number of encounters decreased by 24.7%, group density by 48.5% and population density by 55.5%. There was no significant difference in the group size (Mann-Whitney U Test, $p > 0.05$).

## 3.4 Discussion

3.4.1 Habitat fragmentation and population distribution patternThe detailed census in the central LGS study site showed even higher group and individual langur densities than were revealed by the general Bapen census, suggesting that langur groups had a clumped distribution within LGS. Other examples of highly clumped distributions of primates have been documented, for example, by censuses of gorillas near villages and roads as compared with undisturbed or swamp forest in Central Africa (Tutin & Fernandez, 1984; Blake *et al.*, 1995). In the Bapen Reserve, this clumped distribution pattern may be the result of human disturbance. White-headed langurs living in habitat of lower quality (with more human disturbance) did not reproduce (see Chapter V). Accordingly, they tended to live in or near the central (and less disturbed) habitat and did not use the peripheral habitat.

A comparison between LGS and QN would indicate that white-headed langurs preferred continuous unfragmented habitats. LGS and QN received approximately equal attention from Reserve staff (*i.e.*, were patrolled at similar frequency), so hunting pressure was probably the same in the two areas. The human population density was also similar; it was $70.8/\text{km}^2$ in QN (850 villagers farming in an area of 12 $\text{km}^2$ in size) and $68.4/\text{km}^2$ in LGS (2400 people farming in an area of 35 $\text{km}^2$). QN was so close to LGS that langurs could easily traverse between these two hill-groups. Topography was the only obvious difference. According to studies in the Neo-tropics (Janzen, 1986; Lovejoy *et al.*, 1986; Wilcover *et al.*, 1986), habitat fragmentation resulted in various edge effects, *e.g.*, higher temperature, lower humidity, more sunshine, disappearance of rare plant species, more predation and disease invasion. These effects may make the habitat no longer suitable for rare animal species. Differences in population density in the present study indicated that white-headed langurs preferred large continuous habitat (as in LGS) over fragmented habitat (as in QN). It was also found during behavioural observations that white-headed langurs did not use small habitat fragments.

### 3.4.2 Population density and change over time

Local extinction of white-headed langurs in the Bapen Reserve has been taking place. According to villagers (n = 7, at the age between 75 and 85), white-headed langurs disappeared from GP about a century ago. They occurred in GF until the early 1970s. Thus they might have disappeared from that hill-group about 25 years ago. In MZ, three langur groups were encountered in 1992, but only one group was seen during the present study. The population in LGS has also declined in the three parameters: group size, group density, and population density.

This decline was supported by other information. Langur males emit loud calls, which seem to maintain spacing between groups (see Chapter VI). Higher group density would be expected to cause more inter-group encounters, and therefore a higher frequency of loud calls. Langurs could be heard vocalising about 4-6 times per day in LGS in 1988/89, but only 1-2 times per day in 1997/98 (*pers. obs.*). Local people also commented that langurs were encountered much less frequently than ten years ago.

Factors responsible for this population decline of white-headed langurs in the Bapen Reserve may include habitat loss, habitat degradation, and poaching, Extinction in GP might be related to habitat destruction, because dense bamboo was found there in large amounts, which is an indicator of serious habitat disturbance in the past. Of course, hunting may be involved in the process of extinction in that hill-group. In LGS, data from behavioural observation indicated that langur groups competed for the habitat with high plant species diversity and only about 50% of the study area (533ha) supported reproducing langur groups (Chapter V). Thus, in addition to habitat loss, habitat degradation resulting from tree felling and herb collection may have made an important contribution to the decrease of langur population size in this hill-group. The reason for the extinction in GF is not clear, but hunting contributed at least partly to the disappearance of langurs from the hill-group. According to villagers (n=3), they were hunting langurs moving out to GF from LGS before and during our fieldwork. Poaching was obviously responsible for the shrinking of langur population in MZ, because three of the four police records for poaching were obtained from that hill-group. Habitat quality in MZ was similar to that in LGS (see Chapter II).

In Longgang Reserve, there were about 300 langurs in 1987 (Guangxi Provincial Forestry Department, 1993). Because of the vagueness of this figure and uncertainty about the field technique used, further historical comparison will not be made to indicate the population trend. However, the mean group size, group density and population density were all highest in Longgang (*Table 3- 6*), suggesting that this reserve provided habitat of a higher quality even than the most undisturbed areas in Bapen.

### 3.5 Summary

1. There were 136 white-headed langurs encountered in Bapen Reserve and 73 langurs in Longgang Reserve. Of the 136 langurs encountered in Bapen, 129 lived in 19 groups and 7 were solitary. The 73 langurs in Longgang lived in 8 groups. Data from detailed survey in Bapen show that the population density of white-headed langurs was highest in the central area of the reserve where the reserve staff patrolled most frequently. All the 73 langurs in Longgang were also encountered in the central area where the habitat was well pretected and poaching was prohibited.
2. In Bapen Reserve, langur population was restricted to limestone hills. A total of 5 groups of hills were surveyed and white-headed langurs were mostly found in the hill-group LGS. Thus, LGS was the area that contained the main population pool of langurs and so the main study area was located in this hill-group.
3. In the main study area (*i.e.*, the hill-group LGS), langur population has changed in three parameters from 1990 to 1997: the number of encounters has decreased by 24.7%, group density by 48.5% and population density by 55.5%. Poaching mostly took place outside LGS and was responsible for local extinction of

langurs outside the main population pool. Habitat loss was the main factor causing the decrease in population density inside the main population pool.

Chapter IV

# GROUP COMPOSITION AND ACTIVITY PATTERN

## 4.1 Introduction

Mammals tend to be selective in their times of activity and their spatial use of habitat (SCNP, 1981). While most mammals are nocturnal, the majority of living primates are diurnal (Fleagle, 1999). The amount of time a primate spends in each of its major activities each day is a function of a variety of environmental and physiological constraints (Stanford, 1991).

The concept of time budget is based on the premise that the daylight time available is a limiting factor, in that a primate must carry out its maintenance behaviours in addition to pursuing its social activities (Altmann, 1980). Because of differences in temperature and caloric value of the diet, species spend their active time on different activities, which forms time budgets that may be different from species to species. Thus time budgets have been studied extensively in different primate species (*Cercopithecus sabaeus,* Harrison, 1985; *Colobus badius tephrosceles,* Clutton-Brock, 1974; Marsh, 1978, 1981; *Lagothrix lagotricha,* Defler, 1995; *Macaca fuscata,* Watanuki & Nakayama, 1993; *M. mulatta,* Post & Baulu, 1978; Malik, 1986; *M. silenus,* Kurup & Kumar, 1993; Menon & Poirier, 1996; *Papio anubis,* Bercovitch, 1983; *P. cynocephalus,* Post, 1981; and *Presbytis leucocephalus*, Li, 1992). In these studies, activities are widely classified into the following categories: *feeding* (which may be included in *foraging*), *resting, moving* (or *ranging*), and *grooming*, and all other rarer activities are put in *others* (e.g., Marsh, 1981). Marsh (1981) and Oates (1977) showed that red colobus monkeys and black-and-white colobus monkeys living in peripheral habitat spent less time feeding than in better habitat. In the Anamalai Wildlife Sanctuary, Tamil Nadu (India), two feeding peaks of lion-tailed macaques coincided with two monsoons that caused two peaks of food availability (Kurup & Kumar, 1993). Mating also occurred most frequently during the two peaks. In the same sanctuary, Menon & Poirier (1996) documented seasonal changes in the time budget and a negative correlation between foraging and resting in lion-tailed macaques. Like the colobus monkeys, the lion-tailed macaques spent less time feeding in worse habitat. Japanese monkeys spent more time resting and reduced the time for other activities when the air temperature dropped (Watanuki & Nakayama, 1993). In the eastern Colombian Amazon (Defler, 1995), woolly monkeys showed a seasonal change only in the time budget of social activity, increasing as a function of increased food supply; furthermore, they showed a negative correlation between resting and moving. Thus, primates change their time budgets in three ways to respond to lower habitat quality: (1) increasing resting time but reducing feeding time, (2) increasing feeding time, and (3) keeping maintenance activities constant while reducing time for social activities.

Play is an important social activity for young primates. According to Poirier *et al.* (1978), play has three functions. *(a)* An individual will learn locomotor skills during normal growth and development. *(b)* Through play, the nervous system will be provided with stimuli through sense organs and its development will be stimulated. *(c)* Play behaviour will increase the individual's social experience, encouraging socialisation and development of the whole behavioural repertoire. Play is also a "low priority behaviour' that is suppressed earlier when adverse living conditions occur (Burghardt, 1984), so it is used as an indicator of habitat quality (Martin, 1982; Lee, 1986; Sommer & Mendoza-Granados, 1995). It has been found during several field and laboratory studies on ungulates and primates that play behaviour decreases when food resources decrease (Sommer & Mendoza-Granados, 1995). Based on observation of two male bands of the Hanuman langur (*Presbytis entellus*) in Rajasthan (Northwest India), Sommer & Mendoza-Granados (1995) concluded that play behaviour is a reflection of environmental conditions. The langurs in habitat of better quality spent more time playing. The relationship between habitat quality and play was shown by a strong correlation between the amount of fruit in the diet and time spent on playing. Thus, play is indeed an indicator of energy intake.

It is assumed that, for any particular species, an optimal balance between energy intake and expenditure will have been favoured by natural selection. Any extra use of energy will result in increasing energy intake or reducing energy for other activities. Socioecological factors, such as group size, habitat quality, seasonal variation in food availability, and day journey length, interact and change the time budget through the energy balance (Dunbar, 1992; Menon & Poirier, 1996). To keep the balance, behavioural responses are involved. Due to the low quality of their diet, leaf-eating primates tend to spend a higher proportion of time resting (Rose, 1978) or reduce their feeding time (Oates, 1977; Rose, 1979; Marsh, 1981). A question to be addressed in this chapter is how did the white-headed langur respond to deteriorating habitat? The following three predictions are to be considered.

First, seasonal changes in diet quality may result in behavioural responses. Tropical forests have often been classified as either seasonal or non-seasonal, depending on the degree and annual distribution of rainfall (White, 1998). In the sub-tropical region, temperature fluctuates year-round and rainfall is seasonal. These climatic changes cause differences in food availability and energy expenditure of primates. Primates may respond to the differences in two ways; one is to change their time budgets (see above), the other is to choose different food species or food items. (Seasonal changes in diet will be detailed in Chapter V.) Thus, it is predicted in this chapter that white-headed langurs will respond to the lean seasons by increasing resting time, reducing energy-expensive activities, or reducing feeding time.

Second, time budgets vary among primate groups due to differences in habitat quality of their home range. Habitat quality is usually different between central and peripheral areas of forest, because of sparse vegetation and more human disturbance in the peripheral area (Oates, 1977; Marsh, 1981). Difference in forest types also results in variation in habitat quality, because of differential availability of high quality food (Menon & Poirier, 1996; Menard & Vallet, 1997). Based on this point, it is predicted that white-headed langur groups living in worse habitat will respond in the same way as to seasonal decreases in food availability, *i.e.*, by increasing their resting time and decreasing their feeding time, or time on other energy-expensive activities.

Third, infants and young juveniles have different time budgets from adults (Byrne *et al.*, 1993; Defler, 1995). They tend to spend more time on energy-consuming activities, such as social behaviour (Defler, 1995). The young individuals' high quality food (milk) may be one of the factors that permit them to spend more time on energy-expensive activities, such as play.

Because of different evolutionary history, species have different dietary adaptations (detailed in Chapter V), which indicates that they use foods with different nutritional value. Thus the time budget of a frugivore may be different from that of a folivore. It has been suggested that the proportion of leaves in the diet has a strong correlation with the amount of time resting; *i.e.*, low-energy folivory is related positively to rest behaviour (Dasilva, 1992; Smith, 1977; Rose, 1978, 1979; Morbeck, 1979). Species of *Presbytis* can be classified into langurs (with more leaves in the diet), leaf monkeys (with more fruits and seeds in the diet), and the Hanuman langur (whose diet is intermediate between them) (see Chapter I). Different parts of an individual plant vary in chemical contents, so their nutritional quality is also different (Waterman & Kool, 1994). The amount of leaves in the diet should be positively related to resting time among *Presbytis* species. In this chapter, this relationship will be discussed.

## 4.2 Methods

### 4.2.1 Methodological background – Behaviour sampling

Not all primatologists study behaviour in the same way or ask the same questions. They may study an event or a state, maintenance activities or social interactions. They may work in laboratories or in the wild. Their study animals may be shy or habituated. Some researchers work in mountains while others in grassland. Because of the different questions that they ask and the different observation conditions they have, different techniques have been developed for data collection. Altmann (1974) is widely cited because of her summary of data collection techniques that had been developed and used earlier. In that paper, six techniques for behaviour sampling were summarised, including (1) *Ad libitum*, (2) focal animal sampling, (3) all occurrences sampling, (4) sequence sampling, (5) one-zero sampling, and (6) instantaneous and scan sampling. Martin & Bateson (1986, 1993) proposed a two-step process when deciding on the rules for behavioural data collection (*Figure 4- 1*): first is *sampling rule,* including *ad libitum*, focal, scan and behaviour sampling; second is the *recording rule,* including continuous recording and time sampling.

*Ad libitum* sampling is a non-systematic (opportunistic) sampling. In using this technique, the observer records any behaviour of interest with no systematic time constraints. Usually, only obvious behaviours are recorded. It is often used in initial surveys in the field. It is also used to collect some particular kinds of data, such as deaths, births, inter-group interactions, copulations, group take-overs, and other rare events.

**Focal** and **scan behaviour sampling techniques** are widely used in behaviour research. In using focal behaviour sampling technique, the observer chooses an individual and observes it for a given time period without switching attention to other individuals. Accordingly, (s)he uses continuous recording rule to record any behaviours occurring during the time period. In using scan behaviour sampling technique, the observer quickly scans behaviours of all visible individuals and records these behaviours. Scanning is conducted at time intervals, *e.g.*, every 10min. In this technique, time sampling recording rule is followed. For a field primatologist, observation conditions are often a major concern when choosing a systematic data collection technique. Tree canopies and rocks block observation, so focal sampling technique can be difficult to use in the field (especially in a forest environment). Lack of animal habituation imposes extra difficulty on using focal sampling technique, because it is usually difficult for the observer to identify primate individuals in a short time period. Therefore, scan sampling technique is often used in primate studies in the wild.

In the other two time sampling recording rules, **one-zero sampling** yields data that reflect little of either the duration or frequency of behaviours (Altmann, 1974). Altmann & Wagner (1970) provided a way to calculate frequencies using one-zero scores. This requires that the scores follow a Poisson distribution. If the researcher does not know the distribution pattern of scores or if the scores do not

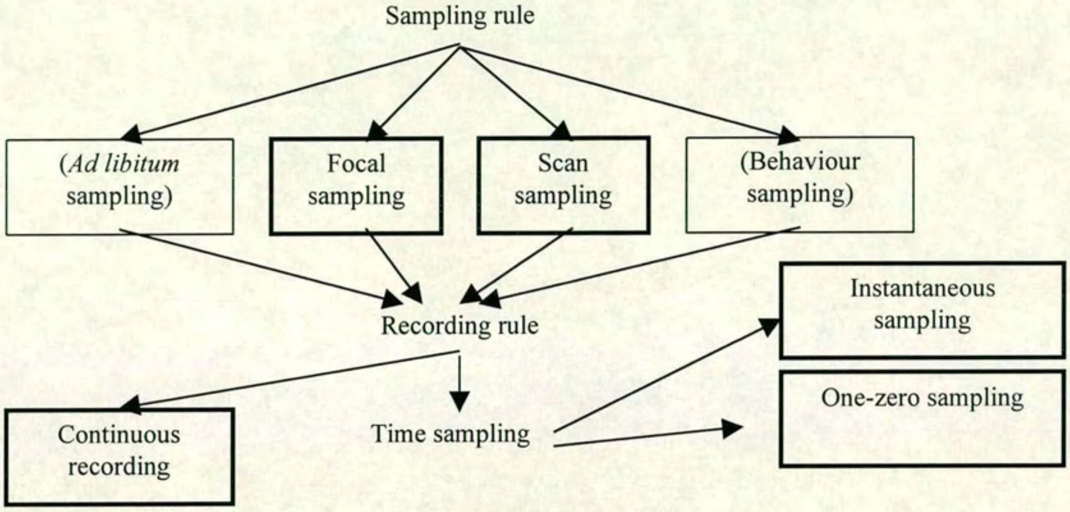


**Figure 4- 1 The hierarchy of sampling rules (determining who is watched and when) and recording rules (determining how their behaviour is recorded). (From Martin & Bateson, 1993)**

follow a Poisson distribution, then there is no basis to use the scores to estimate percentage of time spent in an activity.

**Instantaneous sampling** does not give true frequencies or durations either; instead, it produces scores (Martin & Bateson, 1993); *i.e.*, proportions of records for activities (a record is defined in the following section). These proportions can be used to indicate activity budgets of primate groups. In using this recording rule, the accuracy of data depends on the length of the sample interval; *i.e.*, the accuracy increases with shorter intervals (see Fig. 6.5, Martin & Bateson, 1993). In practice, however, especially if primate groups are large or partially concealed, and the observer cannot maintain concentration for a long time, a longer sample interval is required for field researchers who have to collect data for several activity categories at the same time. Thus a balance must be determined between practical considerations and accuracy. Following Altmann (1974), Stanford (1991) adopted a 10min scan sample interval for his study on *Presbytis pileata*, which ensured that, for events, each scan was discrete from the previous one.

### 4.2.2 Field procedure

Observations were carried out in the main study area (see *Figure 2- 5*). Because of the inaccessible cliffs, a langur group could easily leave an accessible area and was often lost for several days. If only a few groups had been selected as study groups, it would have been very possible that no data would have been collected when all the study groups were out of the area. Therefore it was decided at the outset to identify as many groups as possible, some earlier in the study and others later, rather than concentrating on obtaining more data from one or two groups.

Fieldwork was carried out from September 1997 to September 1998, lasting 13 months. Observational data were collected on activity and diet, using instantaneous scan sampling, with a 10-minute interval between scans. During an observation, the initial sample set was taken 10min after langurs were first encountered. Once timing had started, searching for langurs and recording all data were limited to the first 2min of each time interval. Individuals that were not seen in this time period were marked "absent". Each visible individual was scanned once per sample set. When the locality was known, a code for the height of hill was recorded (for details of the classification of the height of hill, see Chapter II). To avoid disturbing langurs, the observer in most cases stayed concealed. Observation was conducted through binoculars and a spotting scope, because langurs were seldom close enough to observe with the naked eye. A working day began in the morning (around 0720) and ended in the evening (around 1920) with a 3-hour break period around lunchtime (because langurs largely stayed in bush or caves and thus were invisible). When any unusual events occurred (*e.g.*, fighting), systematic data collection was interrupted and details of the events were recorded using *ad lib.* sampling. On completion of the events, no further systematic scan sampling was done on that langur group that day.

A *record* was an observation obtained from an individual. A *sample set* was the set of records obtained by scanning a group of animals in each 10min interval. Its size thus depended on the number of animals in the group. A *case* was one day's collection of sample sets.

Activity categories included *feeding, resting, moving, playing,* and *grooming. Feeding* was recorded when langurs picked food off plants, when they put food into the mouth, and when they were chewing. *Resting* was recorded when animals kept sitting without movement or when they slept. Vigilance and self-grooming were also included in this category. *Moving* was recorded when langurs moved from one site to another site, without chasing. This included when animals changed their sitting places or moved from one site to another site for feeding or resting. *Playing* referred to running about, jumping with or without chasing each other, and fighting without hostility. *Grooming* referred only to allogrooming; that is, one individual groomed another. Foraging was not established as a separate category, because it was not easy to tell the difference when langurs moved to seek for food at other sites and when they moved for reasons other than food. When a langur moved, stopped, and then started to collect food and eat, the observation was recorded as *feeding;* if the langur did not eat after stopping, the observation was as *moving.* All other rarer activities were put in *others* that included presenting, copulation, suckling milk by infants &

young juveniles, feeding milk to infants & young juveniles by adult females, licking rock surfaces, allo-mothering, loud call by adults, screaming by infants and juveniles, shaking trees, urinating, drinking water, chasing and fighting (in conflict).

Information on diet was collected at the same time and included food plant species identity and food items. Identity was indicated by a code (a species no.) that had been established before the data collection on phenology (see Chapter II). Food items included *young leaf, mature leaf, senescing leaf; flower bud, open flower, immature fruit*, *mature fruit,* and *seeds*. Dietary information will be presented in Chapter V.

### 4.2.3 Data analysis

Independence of observational data is always a major concern when the same subjects are observed over time. The violation of data independence occurs in three cases (Martin & Bateson, 1993). 1) *The 'pooling fallacy'* is a common error in behavioural research. Repeated measures that are not independent are treated as independent of one another, so as to give a larger sample size. In such a situation, an additional mistake is to present the number of measures multiplied by the number of subjects as the sample size (n, *i.e*., the number of subjects). 2) '*Litter effects' and other group effects* occur when there is close correlation between animals, such as mothers and their dependent offspring. In such a case, one individual's behaviour influences another's. 3) *Independence of categories* is another common problem arising when different categories are not independent of one another. This can cause problems in interpreting associations between categories. For example, suppose *b* is derived from *a*. *a* and *b* are correlated by definition. In such a case, it is meaningless to test their association.

In addition, the problem of data independence also exists between consecutive scans or days, because the next scan may not be independent from the last scan. In her thesis, McCord (1999) tried to deal with this problem. Based on single scans, each sample interval was coded with a number in sequence. The sample sets were then randomised. Suppose there were N sample sets and M categories, and N/M=R. Along the randomised sequence, the first R sample sets were selected, and the data for the first behavioural category in those sample sets were summed for calculating the time proportion of the first category. The second R sample sets were selected to calculate the time proportion of the second category… And so on. R is determined according to N and M, which will guarantee that there is no overlap between sample sets in calculations of time proportions of categories. That is, there are no sample sets in which data are used for the time calculations of more than one category. By this rearrangement, sample sets and activity categories would become completely independent. This technique was not used for data processing in the present study, because my data were summarised on a daily basis. Most of the sample sets were collected on non-consecutive days. There were only a few cases (7 days versus 217 total days, 3.2%) in which data were collected on consecutive days (see Appendix 1 of this chapter), thus the data for each day could be regarded as independent of one another.

According to Martin & Bateson, it is not always necessary to discard information on within-subject variation. Instead, repeated measurements from the same subject should be averaged to give a single data point for that subject and the sample size (n) should be equal to the number of subjects, not the number of measures. This suggestion was followed in this research.

When an adult carried an infant, the infant's record was excluded from the later calculations so as to avoid *litter effects*, because their activities were not independent. To avoid the problem of the independence of categories, the activity categories were designed to be independent from one another. For example, increase in time feeding would not necessarily cause decrease in time resting, though it would decrease the total time for all other categories.

Records of *absent* individuals were also excluded from the calculations, so the time budget for a given activity category was the proportion of the category's records over the total records of animals seen clearly. Data were processed using the Spearman Rank Correlation Coefficient (Fowler & Cohen, 1992) for testing the associations between variables. ANOVA (discriminant analysis) and the Mann-Whitney U-test were used to test differences in time budgets between groups (Martin & Bateson, 1993). Before the ANOVA test, arcsine transformation was used, because the data were proportions (Fowler & Cohen, 1992). The Kruskal-Wallis test was used to analyse seasonal changes in the time budgets. *SPSS for Windows (Release 6.1.3)* was used in the statistical analyses.

## 4.3 Results

### 4.3.1 Composition of study groups of white-headed langurs

A total of 13 langur groups were identified during the fieldwork. Composition of these groups changed with time due to breeding and other social dynamics (group take-over, migrations, births, and deaths). In the following description, group size is indicated with $n_1$ for that at the beginning of observation on that group and $n_2$ at the end. To simplify nomenclature of groups, a ***band*** indicates a group composed of males only and a ***group*** refers to a bisexual (breeding) group.

**GA1**, identified in the valley LG (*Figure 2- 5*) in September 1997, $n_1 = 4$, including two adult males and two juvenile males. This was a band. Two of them disappeared after October 24, 1997. An unidentified individual joined the band for a few days in February and then again in July 1998, $n_2 = 3$. Observational data were collected from this group for 9 months.

**GA2**, identified in LWG in November 1997, $n_1 = 6$, including an adult male and 5 adult females. No births occurred. A group take-over (*i.e.*, male replacement) took place in July 1998. The group size did not change afterward, though the male had been replaced; $n_2 = 6$. Observational data were collected from this group for 10 months.

**GA3**, identified in LG in November 1997, $n_1 = 13$, including an adult male, 8 adult females, 2 juvenile females, and 2 infant males. Three births occurred in this group: one male between 1-10/12/97, one female between 26/02/-03/03/98, and an infant (sex unidentified) between 08-30/06/98; no infant disappearances were recorded during the whole study period; $n_2 = 16$. This was the largest group studied and one of the major study groups that provided a major proportion of the data. Observational data were collected from this group for 12 months.

**GA4**, identified in LY1 in November 1997, $n_1 = 10$, including 3 adult males (1 old + 2 young), 3 adult females, a subadult male and a subadult female, and two juveniles. A group take-over took place between 12/97-02/98, in which at least 2 young adult males were involved. After the event, this group split into 2 new groups. **GA4-A** included 2 adult males and 3 females; **GA4-B** included 5 adult males, 1 adult female and 1 subadult male. The group size of GA4-A changed from $n_1 = 5$ to $n_2 = 4$ (a female disappeared from the group), and that of GA4-B from $n_1 = 7$ to $n_2 = 9$ (the female disappeared and 3 male outsiders joined). Before the group take-over, there were no fights in GA4; thus it was assumed that the two young males were sons and the old male was the father. The group take-over caused a normal bisexual group to change into a multi-male/multi-female group (GA4-A) and an all male band (GA4-B).

**GALN**, identified in LN in November 1997, $n_1 = 10$, including an adult male, 6 adult females, a juvenile male and 2 infants (1 male + 1 female). There were 4 births between 21/11/97-20/04/98; $n_2 = 14$. The sex of the newborns was not determined. Observational data were collected from this group for 3 months.

**GA5**, identified in LY2 in December 1997, $n_1 = 7$, including 2 males (1 adult + 1 subadult), 3 adult females, 1 subadult male, and 1 infant. There was a birth between 22/01-17/02/98; $n_2 = 8$. This group disappeared soon from its home range in the study area and was not seen again. The disappearance might be related to group GA7 (see below), because approximately at the same time, GA7 was present in LY2 (part of GA5's home range) and LY1. Observational data were collected from this group for 6 months.

**GA6**, identified in LY3 in December 1997, $n_1 \geq 9$, including 1 adult male, 5 adult females, 2 subadults, and 1 juvenile. Five was the minimum number of females counted clearly but there were some others in the forest that were not counted. There were 5 births between 23/12/97-19/05/98; $n_2 \geq 14$. Observational data were collected from the group for 3 months.

**GA7**, identified in LY1 in January 1998, $n_1 = 10$, including an adult male and 9 adult females. There were 3 births between 25/02-08/04/98. One of the infants disappeared between 08/04-20/05 and the other two between 20-30/05/98. Two adult females disappeared between 30/05-28/06/98. An adult female joined the group between 20-29/08/98; thus $n_2 = 9$. Observational data were collected from this group for 9 months.

**GA8**, identified at the entrance of LG in December 1997, $n_1 = 4$, including 1 adult male and 3 adult females. An adult female joined the group between 24/03-03/04/98; $n_2 = 5$. Observational data were collected for 9 months.

**GAGL**, identified in LH in January 1998, $n_1 = 4$, including 1 adult male and 3 adult females. The group composition stayed constant till the end of observation. Data were collected from this group for 2 months.

**GAF**, identified in LLGQ in July 1998. There were two langur forms in the group: white-headed langurs (1 adult male, 2 adult females, and an infant female) and François' langur (*Presbytis françoisi*) (1 adult female); $n_1 = 5$. The François' female looked young, according to her external facial appearance. She might be the one who escaped from a cage at the Reserve Station in May 1996. She stayed on a hill for 3-5 days, and then disappeared. This hill was opposite the Station, and in the hill-group GP (see *Figure 2- 3*). The infant disappeared from GAF immediately after a serious fight around August 25, 1998; $n_2 = 4$. Observational data were collected from the group for 2 months.

### 4.3.2 General pattern of time budget and inter-group differences

Observation was conducted for 982 hrs. There were 2497 sample sets collected, including 19,841 records in total, from 13 identified groups and some unidentified langurs. Of the 19,841 records, 11,013 were the records obtained from langurs that were seen clearly (Appendix B). Only these records were used in calculations. *Table 4- 1* shows a summary of sample sets in each langur group.

Original data were transformed into proportions and used to indicate time budgets of these langur groups in*Table 4- 2*. Based on the 11,013 records, resting

Table 4- 1 Summary of sample sets collected from 13 identified and unidentified langur groups

| groups | Habitat quality* | Group size** | sample sets | records |
|---|---|---|---|---|
| identified | | | | |
| GA1 | | 2-4 | 227 | 411 |
| GA2 | 2 | 6 | 192 | 765 |
| GA3 | 4 | 13-16 | 580 | 3917 |
| GA4 | 3 | 4-12 | 398 | 1607 |
| GA4-A | | 4-5 | 43 | 154 |
| GA4-B | | 5-13 | 140 | 617 |
| GA5 | 3 | 6-8 | 129 | 608 |
| GA6 | 4 | 7-14 | 21 | 122 |
| GA7 | 3 | 5-13 | 137 | 710 |
| GA8 | 1 | 4-5 | 392 | 1350 |
| GAF | | 4+1 | 34 | 105 |
| GAGL | 1 | 4 | 26 | 59 |
| GALN | 4 | 8-12 | 28 | 175 |
| Unidentified | | | | |
| Solo1 | | 1 | 4 | 3 |
| Solo2 | | 1 | 4 | 3 |
| unid1 | | 5 | 21 | 53 |
| unid2 | | 2-3 | 15 | 14 |
| unid3 | | 7 | 8 | 30 |
| unid4 | | 2 | 8 | 16 |
| unid5 | | 8 | 3 | 21 |
| unid6 | | 6 | 28 | 101 |
| unid7 | | 3 | 4 | 2 |
| unid8 | | 4 | 6 | 18 |
| unid9 | | 2 | 12 | 24 |
| unid10 | | 4 | 9 | 28 |
| unid11 | | 5 | 3 | 15 |
| unid12 | | 7 | 6 | 22 |
| unid13 | | 4 | 19 | 63 |
| overall | | | 2497 | 11013 |

* Home range of a langur group often contained more than one class of habitat quality. The quality was scored according to the class that occupied the largest area in the home range.
**For details on group composition, see Section 4.3.1.

accounted for more than 50% of the time budget, and social activities (including *grooming, playing*, and *others*) for only about 20%. *Figure 4- 2* shows the general pattern of annual time budget for these identified langur groups. It must be noted that the real time budget may be different from this, because langurs might be feeding after getting out of sight when data were not collected

Table 4- 2 Annual time budgets of the 13 identified groups as percentage of total records (± S.E.)

| Groups | Feeding | Resting | Moving | Grooming | Playing | Others |
|---|---|---|---|---|---|---|
| GA1 | 13.9±4.5 | 54.7±4.6 | 7.8±2.7 | 18.5±4.3 | 4.9±1.2 | 0.2±0.0 |
| GA2 | 11.1±2.1 | 55.2±3.5 | 13.2±2.5 | 19.2±3.8 | 0.9±0.5 | 0.4±0.3 |
| GA3 | 9.5±1.4 | 51.8±2.8 | 17.8±1.6 | 10.8±1.1 | 8.9±1.1 | 1.1±0.7 |
| GA4 | 14.5±3.0 | 45.1±2.7 | 13.8±2.1 | 24.6±2.6 | 0.9±0.4 | 1.1±0.4 |
| GA4-A | 14.9±6.3 | 56.5±15.6 | 11.0±6.0 | 13.6±5.1 | 3.9±1.9 | 0 |
| GA4-B | 18.0±3.6 | 40.7±4.8 | 20.3±4.2 | 14.1±3.0 | 6.0±1.4 | 1.0±0.5 |
| GA5 | 9.0±1.9 | 56.4±4.2 | 19.1±4.9 | 6.9±1.8 | 8.1±1.9 | 0.5±0.8 |
| GA6 | 2.5±1.3 | 61.5±5.2 | 20.5±4.8 | 0 | 13.1±2.6 | 2.5±2.0 |
| GA7 | 14.5±3.0 | 51.1±4.6 | 15.9±2.6 | 18.2±2.9 | 0.3±0.3 | 0 |
| GA8 | 21.2±2.4 | 46.4±2.9 | 17.3±2.8 | 12.1±1.7 | 1.9±1.0 | 1.0±0.6 |
| GAF | 15.2±8.3 | 41.9±6.4 | 12.4±6.7 | 24.8±12.7 | 0 | 5.7±2.6 |
| GAGL | 16.9±12.9 | 62.7±6.8 | 8.5±3.9 | 10.2±4.0 | 0 | 1.7±1.5 |
| GALN | 13.1±7.1 | 50.9±6.2 | 11.4±3.6 | 3.4±1.6 | 20.0±9.5 | 1.1±1.8 |

Among these groups, GA3, GA4, and GA8 were the most important groups, because their records accounted for 65.9% of the total records. However, data collection from GA4 lasted for only 4 months, which was too short to do further analysis. Thus, GA3 and GA8 were selected for comparison (*Figure 4- 3*).

An ANOVA (discriminant analysis) test showed that these two groups were significantly different in time allocated to different activities ($p < 0.001$), with the greatest differences between the groups in time spent feeding and playing. GA3 spent significantly less time feeding (~ 10% of records) than GA8 (~ 21%) and more time playing (~ 9% by GA3 and 2% by GA8). This was different from the situation in other colobine monkeys, where groups living in worse habitat reduced their feeding time, as an economical strategy in response to the lower habitat quality (e.g., red colobus monkeys and black-and-white colobus monkeys, Marsh, 1981; Oates, 1977). To test this further, data on feeding time from the nine bisexual groups (GA2, GA3, GA4, GA5, GA6, GA7, GA8, GAGL, and GALN, *Table 4- 2*) and on habitat quality

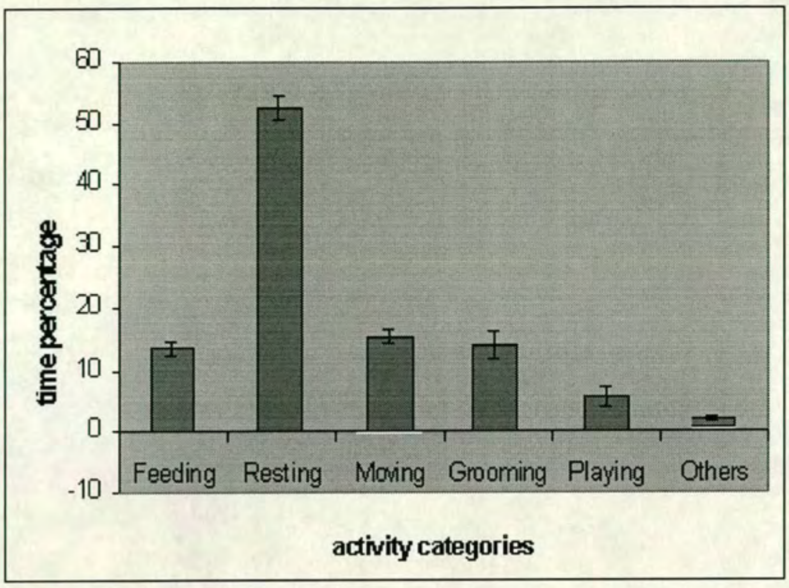


Figure 4- 2 General mean activity budget (mean ± S.E.) of the 13 identified white-headed langur groups.

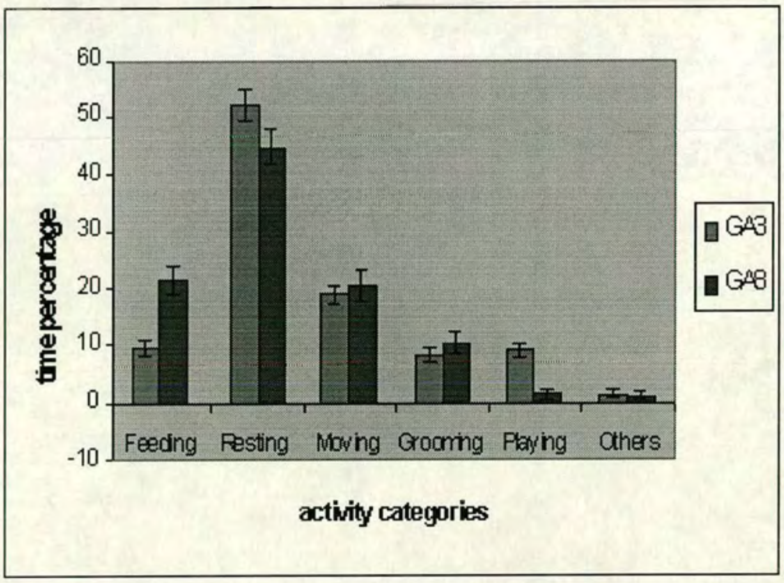


Figure 4- 3 Comparison of time budgets (mean ± S.E.) between GA3 and GA8.

(see *Table 4- 1*) were analysed using the Spearman rank correlation coefficient. The result showed a negative correlation between feeding time and habitat quality ($r_s$ = -.6375, n = 9, one-tailed, $p < 0.05$), which was consistent with the outcome of the comparison between GA3 and GA8. GA3 in better habitat spent less time feeding than GA8 in worse habitat. Resting time was not correlated with habitat quality ($r_s$ = -0.004, n = 9, one-tailed, $p > 0.1$).

A comparison among groups in *Table 4- 2* showed that all-male bands (GA1, GA4-A, GA4-B) spent significantly more time playing (3.9-6%) than bisexual groups without infants/juveniles (GA2, GA4, GA7, GA8, and GAGL, ranging from 0 to 1.9%) (Mann-Whitney U-test, U = 0, P = 0.05). Male langurs with stronger resource holding power (Krebs & Davies, 1997) tended to occupy a higher quality home range, monopolise more females and sire more offspring (Chapter VI). According to Sommer & Mendoza-Granados (1995), langurs in better habitat played more. Group size thus should have a positive correlation with the amount of playing time. *Figure 4- 4* shows the relationship, which was statistically significant (Spearman Rank Correlation Coefficient $r_S$ = 0.589, n=13, one-tailed, $p < 0.025$).

### 4.3.3 Seasonal changes in time budget

Feeding and resting are two alternative strategies of primates to respond to lower habitat quality. Playing time is also an indicator of habitat quality. Thus seasonal variation in the three categories was analysed, using data from GA3 and GA8 (*Figure 4- 5*). Of these activity categories, only playing showed significant seasonal change (see *Table 4- 3*). Because young leaves were the staple food item and feeding on young leaves was seasonal (detailed in Chapter V), a further test was made between feeding time and feeding records for young leaves for GA3. The result did not show a significant correlation (Spearman rank correlation coefficient, $r_S$ = -0.245, n = 11, two-tailed, $p>0.1$). This implies that climatic changes did not influence the feeding and resting time of white-headed langurs, but playing time was significantly influenced. Play is an expensive behaviour in terms of energy, so its seasonality may be correlated with diet. However, there was no significant correlation either between

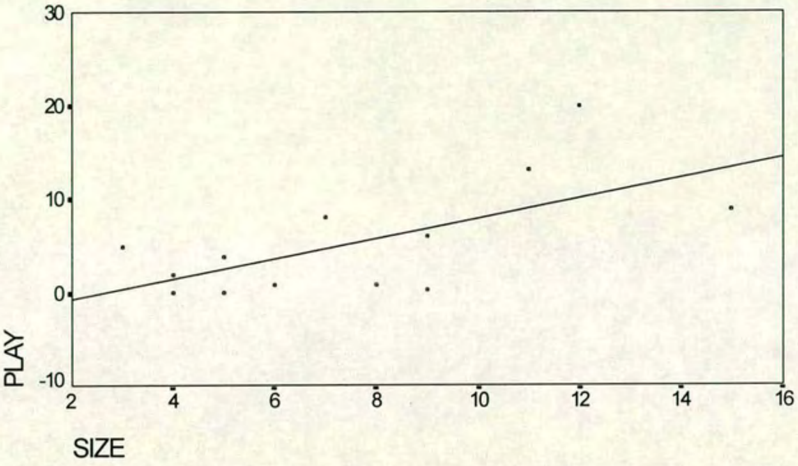


**Figure 4- 4 Correlation between group size (X-axis) of the white-headed langur and playing time (Y-axis, indicated by percentage of play records over the total records). Data from the 13 identified groups were used.**

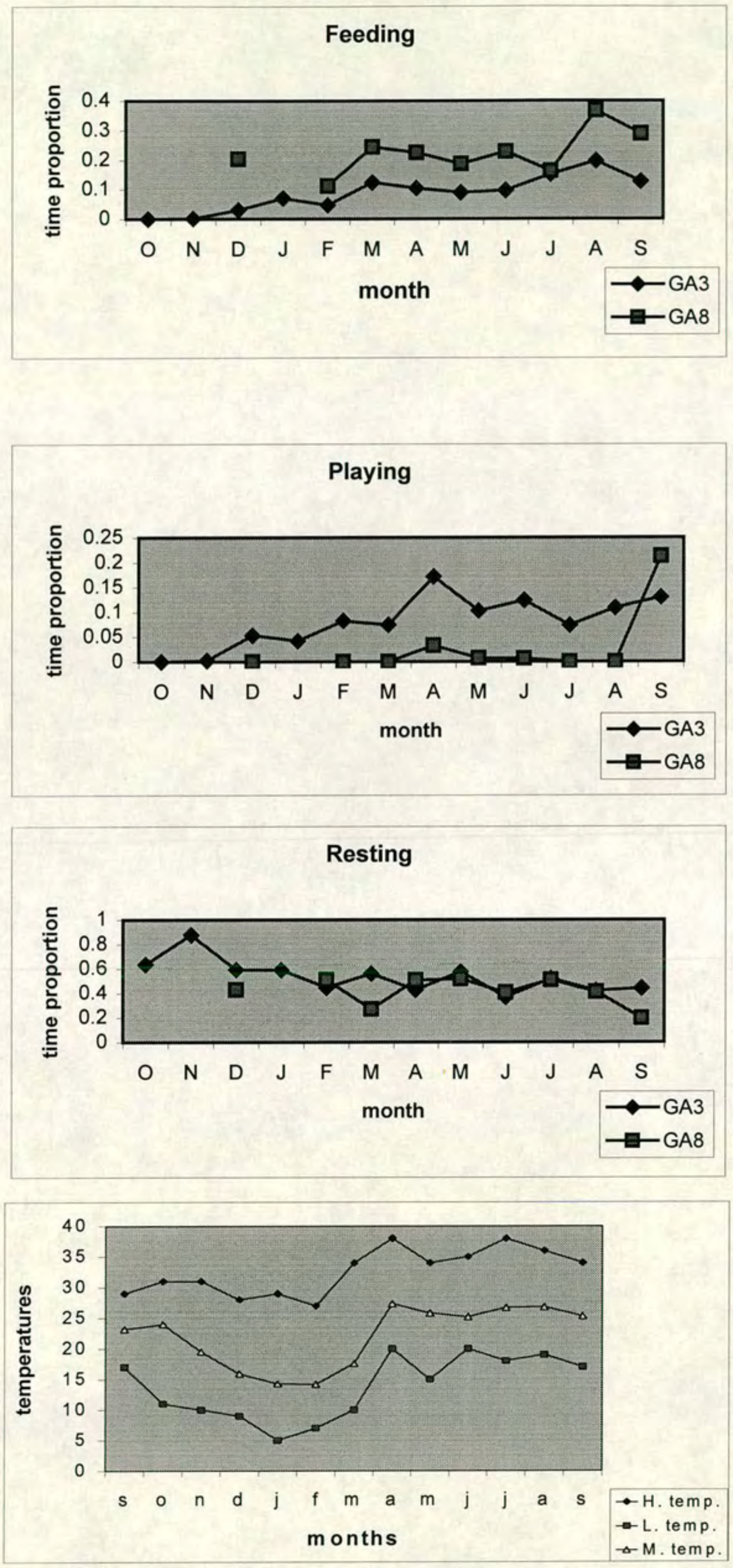


**Figure 4- 5 Seasonal changes in the time budgets of feeding, resting, and playing of GA3 and GA8**

playing and the availability of young leaves ($r_S = 0.182$, n = 12, two-tailed, $p > 0.10$) or between playing and the feeding records for young leaves ($r_S = -0.100$, n = 11, two-tailed, $p > 0.10$). A comparison (*Figure 4- 5*) showed that min temperature and playing time had a similar pattern of seasonal changes. Thus it is suggested that playing was influenced by temperature; *i.e.*, langurs played more when it was warm, which was supported by a significant correlation between these two factors (Spearman rank correlation coefficient $r_S = 0.675$, n = 12, one-tailed, $p < 0.025$). A prominent feature in the playing curve was that it maintained a low level between 10/97-03/98, reached a peak in 04/98, and maintained a relatively high level afterward. April was just at the onset of the summer, so the temperature maintained a high level as well. In the cold weather, infants and juveniles were embraced by adult langurs. In the warm weather, they were freer of their mothers. Of course, effects of maturation may also be involved.

**Table 4- 3 Seasonality of feeding, resting, and playing in GA3 and GA8 (results of the Kruskal-Wallis test)**

| Group | Feeding | Resting | Playing |
|---|---|---|---|
| GA3 | K=16.77, df=10, p>0.05 | K=16.67, df=10, p>0.05 | K=20.62, df=10, p<0.05 |
| GA8 | K=6.28, df=8, p>0.05 | K=10.58, df=8, p>0.05 | K=10.52, df=8, p>0.05 |

### 4.3.4 Intra-group differences in time budget

Because of different nutritional intake, young animals may have a different time budget from that of adults. In GA3, there were all sex-age classes from infants to adults. Because some of the infants became juveniles during the observation period, records from the two age classes were combined together and compared with adults in *Figure 4- 6*. It is seen that, compared to *Figure 4- 2*, the proportions of playing time and moving time have been greatly increased in young animals and, as a result, those for other activities reduced. Discriminant analysis showed that the activity pattern of infants & juveniles was significantly different from that for adults (ANOVA, df = 6, $p < 0.001$). The fact that infants and juveniles spent much more time playing and moving may be used to explain the relationship between langur

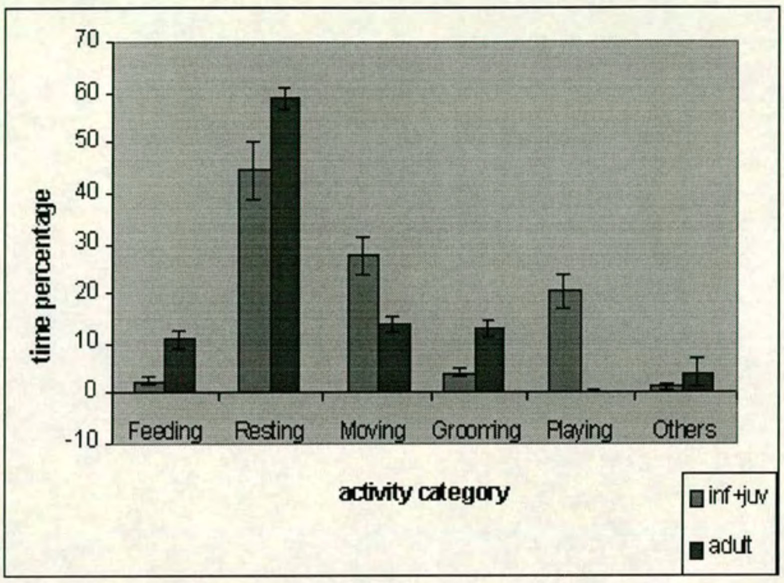


**Figure 4- 6 Comparison of time budgets (mean ± S.E.) between adults and infants + juveniles in group GA3, based on the data collected from October 1997 to September 1998 (12 months). The data were summarised on a monthly basis.**

group size and playing time in *Figure 4- 4*. In large groups, there were more infants and juveniles whose play accounted for a large proportion of group activity. Thus the larger groups in general had a higher proportion of records of play.

A question arises now: Did the habitat quality influence an individual's play regardless of its age, or did it influence the fecundity of a group, through which the playing time was influenced? To test this question, the habitat quality (see *Table 4-1*) and the playing time from bisexual groups without infants & juveniles, GA2, GA4, GA7, GA8, GAGL, were compared, but did not show any correlation (the Spearman rank correlation coefficient $r_s = 0$, $n = 5$, two-tailed, $p > 0.10$). This may indicate that the habitat quality influenced langur group play behaviour by influencing the group's fecundity, rather than group members' activity *per se*; *i.e.*, there were more infants & juveniles in groups in higher quality habitat than in those in lower quality habitat (detailed in Chapter V). Adults also differed from infants & juveniles in their time grooming. Adults spent more time grooming than juveniles and infants.

### 4.3.5 Associations between activities

Moving and playing were energy-consuming activities, while feeding was an energy-obtaining activity and resting an energy-saving activity. They were compared using data collected from GA3 from October 1997 to September 1998. *Table 4- 4* shows associations between these activities. Among these variable pairs, only play and rest had a strongly significant negative relationship ($r_S = -0.797$, $p<0.01$). This means that infants and juveniles increased the time for playing by reducing the time allocated to other activities, especially resting, during the daytime.

**Table 4- 4 Correlation among feeding, resting, moving, and playing (Spearman's Rank Correlation Coefficient $r_S$)**

| | Feeding | Resting | Moving | Playing |
|---|---|---|---|---|
| Feeding | | -0.189, p>0.10 | -0.385, p>0.10 | 0.532, p>0.05 |
| Resting | -0.189, p>0.10 | | -0.434, p>0.10 | -0.797, p<0.01 |
| Moving | -0.385, p>0.10 | -0.434, p>0.10 | | -0.077, p>0.10 |
| Playing | 0.532, p>0.05 | -0.797, p<0.01 | -0.077, p>0.10 | |

* n=12, two-tailed.

### 4.3.6 Rare activities

In the general time budget (*Figure 4- 2*), rare activities (N = 103 records) accounted for about 1% of the total records. These included 16 records of fighting, 18 of infants suckling milk, 20 of licking a rock surface, 31 of loud calls, and 18 of others (including chasing, tree shaking, presenting, allomothering, feeding milk to young by mothers, screaming, urinating, and drinking water). *Table 4- 5* shows the details.

## 4.4 Discussion

### 4.4.1 Time budgets, seasons and habitat quality

As has been mentioned in the Introduction, many species show a seasonal change in their time budgets. In sub-tropical areas, this is because cold weather causes extra energy expenditure to keep body temperature constant in the winter. However, only play showed a significant seasonal change in white-headed langurs, whereas all other activity categories did not.

There are three ways in primates to change their time budgets as a response to lower habitat quality or lean seasons. First is to increase resting time (*e.g.*, *Colobus polykomos*, Dasilva, 1992; *Macaca sylvanus,* Menon & Poirier, 1996; *M. fuscata,* Watanuki & Nakayama, 1993). Second is to reduce feeding time (*e.g., Colobus badius* and *C. polykomos,* Oates, 1977; Marsh, 1981). Third is to reduce time for social activities while maintaining the maintenance activities constant (*e.g.*, the woolly monkey *Lagothrix lagotricha*, Defler, 1995). White-headed langurs had a time budget similar to that of the woolly monkey. In the woolly monkey, juveniles and infants contributed most records for the total social behaviour (including playing). Adult woolly monkeys played little. In the present study on white-headed langurs, play accounted for the major part of social behaviour in juvenile and infant langurs. Similar to the woolly monkeys, juvenile and infant white-headed langurs contributed most records for the total play behaviour and adult langurs played little. In contrast to lion-tailed macaques, Japanese macaques, red colobus, and black-and-

Table 4-5 Distribution of rare activities in the langur groups (number of records and the percentage)

| Groups | A-M | Ch | F-M | Fi | L-C | M-S | Pr | R-L | Sc | T-S | U | W-D | Total | % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GA1 | | | | | | | | | | 1 | | 1 | 2 | 1.9 |
| GA2 | | | | | 1 | | 3 | | | | | | 4 | 3.9 |
| GA3 | | 2 | 1 | | 20 | 14 | 1 | 3 | 3 | | | | 44 | 42.7 |
| GA4 | | | | 14 | 1 | | | | | | | 2 | 17 | 16.5 |
| GA4" | | | | | 3 | | | 2 | | | 1 | | 6 | 5.8 |
| GA5 | | | | | 3 | | | | | | | | 3 | 2.9 |
| GA6 | | | | 2 | 1 | | | | | | | | 3 | 2.9 |
| GA8 | | | | | | | 1 | 12 | | | | | 13 | 12.6 |
| GAGL | | | | | 1 | | | | | | | | 1 | 1.0 |
| GALN | | | 1 | | | 1 | | | | | | | 2 | 1.9 |
| GAF | 1 | | | | | 3 | | 2 | | | | | 6 | 5.8 |
| Unid.6 | | | | | 1 | | | | | | | | 1 | 1.0 |
| Unid.13 | | | | | | | | 1 | | | | | 1 | 1.0 |
| Total | 1 | 2 | 2 | 16 | 31 | 18 | 5 | 20 | 3 | 1 | 1 | 3 | 103 | |
| % | 0.97 | 1.94 | 1.94 | 15.53 | 30.10 | 17.48 | 4.85 | 19.42 | 2.91 | 0.97 | 0.97 | 2.91 | | 100 |

A-M: allo-mothering behaviour; Ch: chasing; F-M: mother feeding milk to infant; Fi: fighting; L-C: loud call; M-S: infant suckling; Pr: presenting; R-L: licking rock surface; Sc: screaming; T-S: shaking trees; U: urinating; W-D: drinking water. The number of records for *F-M* was not necessarily equal to the number of records for *M-S*, because when the mothers ate or groomed while her infant/juvenile was suckling, the mother's activity was recorded as *F* or *G* but not *F-M*.

white colobus, the white-headed langur and the woolly monkey adopted the third way in response to lean seasons. The daily low temperature was the main reason causing the seasonal change in play in the white-headed langur. The seasonality of births may be another reason; *i.e.*, infants born between February and April grew up in warm weather (detailed in Chapter VI) and spent a great amount of time playing during their growth. Data on feeding ecology indicate that the constant time budget of adult langurs through the seasons may be attributable to the availability of some species of fruit in the winter (detailed in Chapter V).

In a given species, animal groups occupy home ranges with different habitat quality. Thus the habitat provides foods to the animals with different nutritional value. Leaf-eaters respond to the low nutritional value of leaves by increasing the time spent resting and by reducing time for other activities, so as to save energy. Groups of *Colobus badius* and *C. guereza* living in peripheral habitat (where vegetation is sparse and the monkeys are more disturbed by people) tend to spend less time foraging and more time resting than those conspecifics living in better habitat (Marsh, 1981). In contrast, white-headed langurs in worse habitat spent more time feeding.

Because play is soon suppressed when adverse living conditions occur (Burghardt, 1984), it is a sensitive indicator of habitat quality (Sommer & Mendoza-Granados, 1995). Members in all-male bands of the Hanuman langur (*P. entellus*) in better habitat played more than in worse habitat, and playing had a positive correlation with amount of fruits in their diet. In the present study, however, play was significantly correlated to group size only. Better habitat supported larger groups with more infants and juveniles who contributed more to the records of play. It did not increase playing records for adult langurs, but increased the records for the groups as a whole by increasing the groups' fecundity. Indeed, adult langurs spent little of the daytime playing. This result seemed to be different from the findings of Sommer & Mendoza-Grannados (1995). As in the Hanuman langur, all-male bands of white-headed langurs played more than bisexual groups and thus were good observation subjects for testing this finding. Unfortunately, there were not enough data collected from the all-male bands for statistical analysis.

The high nutritional value of the diet of infants and young juveniles allows young animals to engage in more energy-consuming activities. In *Macaca sylvanus* (Menard & Vallet, 1997) and *L. lagotricha* (Defler, 1995), juveniles and infants in general spend less time feeding and more time in social interaction than adults. In the present study, white-headed langur infants & juveniles spent significantly more time playing than adults (*Figure 4- 6*). Because of its three major functions (see Introduction to this chapter), play is necessary to young individuals during their physical and behavioural development and socialisation. A difference in time budget between adults and young individuals seems to have a selective advantage. Play is an expensive behaviour in terms of energy expenditure; *i.e.*, this behaviour consumes energy but does not bring energy. It may impose extra pressure on animals to retrieve energy from the habitat. Thus habitat quality may be vital for production of offspring. Lack of infants and juveniles in worse habitat (Chapter V) may indicate that the habitat is unable to provide sufficient nutrients to support reproduction in female langurs. In such a situation, they increased feeding time and stopped producing offspring.

### 4.4.2 Time budgets and folivory

Due to different evolutionary history, species have different dietary adaptations. Because of this, they spend different amounts of time resting. Folivorous primates in general spend more time resting than frugivorous and insectivorous primates. For example, the capped langur (*P. pileata*) spent 40% of their active (= daylight) time resting, and leaves (sum of different parts) accounted for 57.8% of the species' annual diet (Stanford, 1991). In the white-headed langur, time spent resting ranged from 51% (*Figure 4- 2*) to 69.1% (Li, 1992) of the daytime. Leaves accounted for over 80% of the species' annual diet (Chapter V). In contrast, fruit eaters spend less time resting (*e.g.*, *Macaca mulatta*, 30% to 39.2% of time resting, Post & Baulu, 1978; Malik, 1986; *M. silenus*, 16%, Menon & Poirier, 1996). In addition to higher nutritional value, patchy distribution of fruits may also increase moving time and thus reduce resting time of these frugivorous monkeys. A large amount of resting time seems to be a behavioural adaptation to a diet of low nutritional quality, and is thus a typical characteristic of leaf-eaters, which may be explained on the basis of digestion constraints (Dasilva, 1992). Primates with more leaves in the diet need more time for digestion (Kay & Davies, 1994), because fibre and secondary compounds are usually difficult to break down, so leaves are retained in the digestive tract longer than fruits. The longer time allows microbes to ferment the fibrous content that is then digested by enzymes produced and absorbed by the digestive tract. This explanation is also supported by the functional anatomy of the gastrointestinal tract, which is specialised for foregut fermentation in colobines (Chivers, 1994).

### 4.5 Summary

1. White-headed langurs spent an average of 51% of each day resting, 13% feeding, 16% moving, 14% grooming, 5% playing, and only 1% for other rare activities. Compared to other primates, it seems that the high proportion of resting time was related to the high proportion of leaves in the diet.
2. Time budget of adult white-headed langurs did not show a seasonal change. Only play by infants and juveniles showed a seasonal change. It was correlated at least with low air temperature. The constant time budget may be explained using data on feeding ecology.
3. Time budget changed with age. It was characterised by an obvious increase in playing time in infants and juveniles (5% in the general pattern vs. 25% in infants and juveniles). Infants and juveniles increased playing time by reducing resting time.
4. Time budget varied significantly among different groups of the white-headed langur as well. Groups in better quality habitat spent more time playing and feeding and less time resting. Only playing time of infants and juveniles was influenced by habitat quality and that of adult langurs was not.

Chapter V

# FEEDING ECOLOGY AND HABITAT USE

## 5.1 Introduction

The goal of this study was to provide options for improved conservation of white-headed langurs in the wild. For this purpose, the basic ecological requirements of langurs were explored, in particular their feeding ecology and habitat use.

### 5.1.1 Feeding ecology

Colobine monkeys are leaf eaters to a variable extent (Waterman & Kool, 1994) and have evolved some morphological adaptations to their folivorous diet, such as an enlarged multi-chambered stomach (Chivers, 1994). The leaf-eating diet poses a problem for digestion. Tannins from the food interact with proteins to form insoluble complexes, and thus are major digestion inhibitors. This was once considered a non-specific and irreversible reaction. However, recent detailed studies reveal that tannins do not interact equally with all proteins (Hagerman & Butler, 1981; Mole & Waterman, 1987). Furthermore, endogenous surfactant substances have recently been found in the guts of some insects and mammals, although there are few data from *Presbytis* species (see Waterman & Kool, 1994, for a review). Surfactant substances have long been known to interfere with the formation and precipitation of tannin-protein complexes.

The uneven distribution of tannins and other secondary compounds might impose constraints on food selection by leaf-eaters. In general, langurs prefer foods rich in protein and energy and avoid those high in insoluble fibre, tannins, toxins, and other secondary compounds. A report on *Presbytis pileatus* suggests that this species prefers young leaves and fruit, though mature leaf parts account for more than 40% of the diet (Stanford, 1991). Mature leaves are not preferred by langurs, but are eaten at times when young leaves and fruit are not available. This preference seems to be related to differences in chemical components between young and mature leaves

(Waterman & Kool, 1994). The normal pattern is towards lowering nitrogen content, often by as much as 50%, and increasing structural components (fibre and lignin) during leaf maturation. The Tana River red colobus monkeys (*Procolobus badius rufomitratus*) show a tendency to prefer high protein content and avoid fibre (Mowry *et al.*, 1996). Young leaves that make up a large percentage of their diet are significantly higher in nitrogen and lower in acid detergent fibre than more abundant mature leaves. When mature leaves are eaten, red colobus concentrate on leguminous species that are high in nitrogen and low in fibre. A similar tendency is also found in the proboscis monkey (*Nasalis larvatus*) (Yeager *et al.*, 1997).

In addition to eating leaves, animals of *Presbytis* species also eat fruits. Some species (e.g., *P. melalophos,* more than 50% of its diet) eat more fruits than others (e.g., *P. obscura,* less than 50% of its diet) (Waterman & Kool, 1994). While generalisations about the relationship between leaf selection and biochemistry are easy to make, they are more complicated in the case of fruits. At Sepilok and Kuala Lompat (Asia), *P. rubicunda* and *P. melalophos* feed on fruits with a low content of protein (Davies *et al.*, 1988). Data for *P. hosei* shows that lipids in fruits may determine fruit selection (see Waterman & Kool, 1994), because there is an appreciable amount of fat in their fruit food. However, selection for fruits of *Teclea nobilis* (Rutaceae) by *Procolobus badius tephrosceles* at Kibale (Africa) is related to a higher protein content in the fruits, and calorimetric energy measurements suggested that high energy content does not seem to be selected for (Waterman & Kool, 1994).

Seed-eating is related to fruit-eating. It is reported for *P. pileatus* (Stanford, 1991), *P. obscurus* and *P. melalophos* (Curtin, 1980; Bennett, 1983), *P. thomasi* (Ungar, 1995), *P. rubicunda* (Davies *et al.*, 1988; Davies, 1991), *Colobus polykomos* (Dasilva, 1992), *Cercopithecus pogonias* and *C. wolfi* (Gautier-Hion *et al.*, 1993), and for other primate species (for a review, see Garber & Kitron, 1997). A study on *Colobus polykomos* (Dasilva, 1992) suggested that the adaptations the monkeys show to periodic shortages of high energy foods (seeds) are behavioural rather than physiological. A comparative study on *Cercopithecus pogonias* in Gabon and *C. wolfi* in Zaire suggested that soil conditions influence these monkeys' feeding ecology (Gautier-Hion *et al.*, 1993). Monkeys in Gabon are mainly seed-dispersers due to the greater abundance of fleshy fruits in Gabon, whereas monkeys in Zaire are seed-predators due to the low availability of fleshy fruits caused by the poor soil conditions in Zaire. This indicates that the classification of seed-predators and seed-dispersers is not absolute all the time. Food availability may play an important role in forming a primate's feeding strategy.

While several primate species are reported to be seed dispersers, *e.g.*, *Saguinus fuscicollis, S. geoffroyi, S. mystax, Cebus capucinus, Alouatta palliata, Ateles paniscus, Cercopithecus mitis, C. ascanius, Macaca fascicularis, Papio anubis, Pan troglodytes,* and *Gorilla gorilla* (cited from Garber & Kitron, 1997), all colobine monkey species so far studied are seed predators. Several explanations have been proposed for seed dispersal activity. The first is that fruits of some species have fibrous or gelatinous pulp or arils that may be mechanically difficult to remove from the seed. To swallow it may increase the rate at which pulp is ingested and minimise the time spent handling food. The second is that it will enhance feeding efficiency so as to reduce the time that the animals are exposed to risk of predation. The third is that the large size and volume of seeds serve a mechanical function to expel parasites from the digestive tract (Garber & Kitron, 1997; Dew & Wright, 1998).

The importance of seed predation in colobine diets varies considerably (see Bennett & Davies, 1994; Oates, 1994). It seems likely that seed selection will prove more difficult to rationalise in biochemical terms than leaf selection, for a number of reasons (Waterman & Kool, 1994). First, seeds represent a more variable nutrient package than leaves and some of the potential combinations, although appearing to be of high nutritional value, may be unacceptable to the rumen microflora. Second, seeds are likely to be more concentrated sources of toxins than are leaves. And third, seeds present greater handling problems, either because of mechanical protection or because they are surrounded by an unacceptable fruit covering, such as the terpene-rich resins of the pericarp of many dipterocarps. According to Janzen (1974) and McKey *et al.* (1981), seed-eating is an adaptation of colobine monkeys to plants growing on poor soils. As replacement of leaves eaten by herbivores would involve greater cost to these plants, the plants have evolved secondary compounds (*i.e.*, digestion-inhibitors) in leaves. Seed-eating is more common among colobines (*Colobus angolensis* and *C. badius*) living in areas where soils are poor in Zaire (Maisels *et al.*, 1994). In coastal Cameroon, soils are extremely sandy and low in plant nutrients. *C. satanas* lived on trees growing on these soils and ate a high proportion (53% of the diet) of seeds (McKey *et al.*, 1981), whereas *C. badius* ate a large amount of leaves of trees growing on the fine textured soils richer in nutrients in Uganda (Gartlan *et al.*, 1980). Trees in the Cameroon site had a high overall level of tannins and phenolics and low level of nutrients. At the Uganda site, the vegetation was indeed lower in chemical defences. However, *C. satanas* ate more seeds (60%) in Lopé, Gabon, although the soils and plant chemistry in Gabon were similar to the Uganda site (Harrison, 1986), which is not consistent with the prediction from the above hypothesis.

Species in the genus *Presbytis* are regarded as belonging to three subgenera (see Chapter I): *Presbytis* (leaf-monkeys), *Trachypithecus* (langurs), and *Semnopithecus* (Hanuman or grey langur). Diet is one of the differences between these three taxa (Bennett & Davies, 1994). Fruits and seeds account for a large proportion of the diet of grey langur and leaf-monkeys, but much less in the diet of *Trachypithecus* langurs. Furthermore, mature leaves contribute around 30% of the diet of grey langur, but only 1-10% in leaf-monkeys. Meanwhile, leaf-monkeys in Kuala Lompat (Malaysia) and Sepilok (Indonesia) eat seeds of some plant species and discard other parts of the fruit, whereas grey langurs in Simla, Kanha (India), and Polonnaruwa (Sri Lanka), eat seeds along with other fruit parts. The soils at Sepilok (as well as in the whole Borneo) are generally very poor and low in nutrients (Davies & Baillie, 1988), and seeds account for an important portion (as high as 30%) of the diet of *P. rubicunda* (Davies, 1991). This appears to support the hypothesis on the relationship between poor soils and seed-eating.

To keep a balance between energy intake and expenditure, primates change their time budgets as a response to seasonal climatic changes or changes in food availability. A high proportion of resting time is a typical characteristic of leaf-eating primates (see Chapter IV). Seasonality of feeding ecology has been reported from various primate species (Newton, 1992; Kool, 1993; Peres, 1994; Wrangham *et al.*, 1998; Conklin-Brittain *et al.*, 1998; Knott, 1998; Davies *et al.*, 1999; Zhao, 1999). According to Zhao (1999), Tibetan macaques (*M. thibetana*) ate bark and bamboo leaves and reduced the time moving in the winter when food resources were scarce. Young leaves were the staple food item of *P. auratus* from October to December, after which flowers and fruits made a more important contribution to the diet (Kool, 1993). Studies on such dietary changes have become an important aspect of current primatology (White, 1998), because the dietary changes have caused variations in life history and behaviour (Watts, 1998; Zhao, 1999). It was shown in this study that adult white-headed langurs did not change their time budgets significantly in response to climatic change or change in food availability, and only infants and juveniles showed seasonality in play behaviour. However, the langurs may change their food items or food species as a response to seasonal changes. This question will be explored in this chapter.

Evolution of life history is a major concern in evolutionary ecology (Ricklefs, 1990). Life histories bring information on the adaptive success of organisms with particular morphology and physiology, thus they are closely related to the process of extinction of species. Because of this, study of life history is also an important aspect of conservation biology (see Lacy, 1994). It is largely a legacy of David Lack who called attention to the fact that songbirds in the tropics laid fewer eggs per clutch – 2 or 3, on average – than their counterparts at higher latitudes – generally 4 to 10, depending on the species (Moreau, 1944). He clearly recognised the relationship between the ability of adults to gather food for their young that was genetically determined and clutch size. Life history theory developed rapidly during the 1960s (Ricklefs, 1990).

Life history is defined by Lincoln *et al.* (1982) as the significant features of the life cycle through which an organism passes, with particular reference to strategies influencing survival and reproduction. This broad definition has been narrowed down to the study of adaptation using variables in a life table (Ricklefs, 1990), such as fecundity, survivorship, and mortality at specific ages, and migration. Harvey *et al.* (1987) found that the life history of primate species within subfamilies is similar, but varies between subfamilies. They also proposed that body and brain sizes are two important factors causing differences in life history; they tend to be smaller in folivorous primates (see also Clutton-Brock & Harvey, 1980). In this chapter, these two factors will be discussed in relation to variations in diet of *Presbytis* species.

### 5.1.2 Habitat use

Habitat use includes three aspects: the activity budget discussed in Chapter IV, feeding ecology, and spatial use of the habitat (SCNP, 1981).

Ranging behaviour establishes and maintains a primate group's home range. Factors influencing ranging patterns have been extensively studied in various primate species. These factors include the position of sleeping trees (Crook & Aldrich-Blake, 1968; Tenaza, 1975; Rasmussen, 1979; Gittins & Raemaekers, 1980), water holes (Altmann & Altmann, 1970), the weather (Chivers, 1974; McKey & Waterman, 1982), the need to patrol territorial boundaries (Whitten, 1982), the group's movements on previous days (Fossey & Harcourt, 1977), and inter-group interactions (Struhsaker, 1975; Waser, 1976; Isbell, 1983). Species may be affected by these factors in different combinations due to their specific biological/ecological features. Although relationships between food distribution and ranging are complicated by factors such as body size and the form of locomotion, leaf-eating primates in general tend to travel less than fruit-eating primates because of the highly dispersed distribution pattern of fruits (Oates, 1987). Amongst primates in general, and also within the Colobinae, there is a negative relationship between the proportion of the day spent moving and the proportion of foliage in the diet (Newton & Dunbar, 1994; Figure 17-4 of Oates, 1987). For this reason, leaf-eaters have a smaller home range than fruit-eaters. The situation seems more complicated in *Presbytis* species. Day range lengths are correlated with availability of preferred foods in *P. melalophos* (Bennett, 1986). The distribution of the most important food trees is a major influence on range use by *P. entellus* (Newton, 1992). The ranging pattern of these two species is generally influenced by food availability. *Presbytis* species show a wide array of diets from more folivorous to more frugivorous. The subgenera *Presbytis* and *Trachypithecus* (the former is more frugivorous and the latter is more folivorous) show less flexibility in ranging patterns and there is no simple correlation between diet and ranging pattern (Bennett & Davies, 1994). In the capped langur, however, lone animals apparently travelled faster as a tactic to avoid danger rather than to find food (Stanford, 1991).

Home range size is remarkably different in colobine monkeys, ranging from 2-3ha (*Presbytis senex* in Polonnaruwa, Hladik, 1978) and 2ha (*Colobus guereza* in Kibale Forest, Dunbar, 1987) to 5,100ha (*Rhinopithecus roxellana* in Wolong, Hu *et al.*, 1980). The home range size of *Rhinopithecus* and *Nasalis* is larger than that of *Simias, Presbytis, Procolobus,* and *Colobus* (Kirkpatrick *et al.*, 1998). A positive correlation is found between home range size and group (/troop) size in some studies (the Madhupur capped langur, Stanford, 1991; *Macaca fuscata* and *Colobus guereza,* Takasaki, 1984). Furuichi *et al.* (1982) further propose an elastic enclosure model to describe the relationship: $QR = \alpha N$, where $\alpha$ is a constant, Q the habitat quality (scored using vegetation types or extent of habitat disturbance by humans), R the home range size, and N the group size. This equation predicts that the home range size increases proportionally with the group size in homogenous habitat. When habitat quality decreases, a group will have a larger home range to maintain a stable group size. It is assumed that this equation is reasonable, because lower habitat quality indicates less food resources in the home range (Sommer & Mendoza-Granados, 1995).

### 5.1.3 Conservation issues

In addition to vegetation clearance that caused habitat loss in Bapen Reserve (Chapter II), local people were permitted to enter the reserve to cut fuel trees, collect herbs and tree roots (for medicinal use), and search for other natural products. All these activities involved tree felling. The Reserve staff said that white-headed langurs ate young leaves, so permitting peasants to conduct all these activities would benefit the langurs, because, on the one hand, cutting would encourage young leaves to grow; and on the other hand, the needs of peasants would be met. However, habitat degradation may result from the felling, and this effect was not considered in conservation management of Bapen Reserve.

In this chapter, I will explore the dietary adaptations of white-headed langurs to the habitat, competition for resources among langur groups, and the influence of habitat quality on langur survival. Additionally, the conservation implications of feeding ecology and habitat use will be discussed, because the main objective of this research was to provide options for conservation management of white-headed langurs.

## 5.2 Methods

### 5.2.1 Field procedure: feeding ecology

Fieldwork was carried out in the main study area (Chapter II). Scan sampling at ten-minute intervals was used in data collection (see Chapter IV). During recording, food plant species identity and the food items were noted down when feeding was recorded. The food plant species coding system and the classification of food items used in the data collection on phenology (see Chapter II) were used in this work. While eating, langurs sometimes stayed on the rock behind trees and the food plant species identity was not seen clearly. Food items from some tree species were so small that they could not been seen clearly either. In such cases, the identity and item were recorded as *unknown*.

All data presented in this chapter on diet used the percentage of feeding records. The measure was therefore feeding effort rather than food intake. Chivers (1974) used estimates of feeding rates and wet food weight to quantify diet more precisely, since food weights for different types of plant will vary. This technique was not followed in this study, because cliffs prevented the observer from collecting remaining food uneaten by langurs after a meal. The fresh weight of food eaten thus could not be estimated. The feeding effort method was considered acceptable (Stanford, 1991) and is also consistent with most other studies of colobine behavioural ecology (Struhsaker, 1975; Oates, 1977; Davies, 1984; Stanford, 1991), so it allows comparisons with other field data.

A further question is related to seed predation: do langurs digest fruit pulp only or do they digest the seeds as well? To tackle this question, I examined visually

10 faecal samples collected randomly each month from November 1997 to September 1998, trying to find any excreted seeds or seed fragments.

### 5.2.2 Field procedure: habitat use

Before the fieldwork, a map of the main study area was prepared at a scale of 1:5000. The map was covered with a grid system, of which a cell was equal to 1 ha. Cells were numbered using row and column codes. During observational data collection, the position of the study group centre was recorded using the grid coding system after every three scans. Opportunistic encounters were also recorded. These records were plotted on the map to give an estimate of the day range and home range size of each study group during the study period (SCNP, 1981; Fleagle, 1999).

There are several techniques to define the area of a home range, including *minimum convex polygon*, *95% probability ellipse, cluster analysis*, and *harmonic mean,* (Harris *et al.*, 1990; White & Garrott, 1990). Of these techniques, the minimum convex polygon is the oldest and most common method (White & Garrott, 1990) and more robust than other techniques (Harris *et al.*, 1990). It was used in the present study on white-headed langurs. The boundary of a home range was defined by connecting the outer locations to form a convex polygon of minimum area. The home range size was then calculated by counting the number of cells within the boundary. Flat ground in some valleys was excluded from the counting, because it was not used by white-headed langurs.

Radio-transmitters have been used in other studies on home range use (e.g., *Macaca thibetana*, Zhao, 1999; bamboo lemur species of the genus *Hapalemur*, Tan, 1999). This involved trapping animals. In my study, however, trapping animals would have influenced the langurs' ranging behaviour. Furthermore, immobilisation is very dangerous to langurs moving on hill cliffs, so the technique was not used. The study groups therefore were not monitored all the time and the frequency of their presence in a given cell was not considered. To do so would be misleading because of differing observational conditions. For example, there was dense vegetation in the valley LGT that was exclusively used by the group GA3. However, because of its poor observation conditions, no behavioural observations were done, so there were only a few recordings for this group present in that valley. The area of range use represented a minimum, because the langur groups travelled out of the core study area.

The limestone topography caused extra difficulty in measuring the distance that the langurs travelled. In this study, the number of cells entered was used to indicate travel distance. If the langurs stayed in a cell, they were regarded as not having travelled. If they travelled from one cell to a neighbouring cell, they were judged to travel for 100m. When they travelled from a cell through a neighbouring cell to another neighbouring cell, they travelled for 200m. When they repeatedly travelled between two neighbouring cells, they travelled for only 100m. Meanwhile, because it was possible only in a few cases to follow a langur group for a full day, it may be misleading to calculate daily range length using data from the observations conducted in a small section of a day. Thus, the daily range length was not calculated in this study; instead, hourly range length was considered.

In each scan, information on the height level of each visible individual on the hills was recorded (Chapter IV). These records gave a score for each height level of the limestone hills that white-headed langurs used. This information was used to assess the habitat use by langurs in the vertical dimension.

### 5.2.3 Data analysis

All records obtained during behavioural observation were transformed into proportions for non-parametric analysis and further transformed into percentages for reporting. Arcsine transformation was made from proportions for doing parametric statistical analysis (Fowler & Cohen, 1992). Data from the langur group GAF were excluded from analyses, because this group contained one François' langur. In analyses for habitat use, only bisexual white-headed langur groups were involved, including GA2, GA3, GA4, GA5, GA6, GA7, GA8, GAGL, and GALN, totalling 9 groups.

*Staple taxa* (species or family) were defined as those plant taxa whose feeding records made up an overall percentage of over 50% of the total feeding records. For example, food plant species are arranged from the highest to the lowest in terms of their feeding record percentage. If the feeding records of the first 5 species make up more than 50% of the total feeding records, these 5 species are regarded as the staple species. *Preference index* (P-index) was calculated to indicate the degree of preference of a food plant species or a food item using percentage of feeding records divided by percentage of the species individuals over the total individuals or percentage of the item scores over the total phenological scores. *Highly preferred species* (*food item*) were defined as those with P-index $\geq 10$. The Shannon-Weaver Index and the Simpson Index (Ricklefs, 1990) were calculated to indicate the food plant species diversity, and the Shannon-Weaver Index was used for statistical analysis on differences in the diversity between groups and the seasonality of diet. For details of calculation of these two indices, see Chapter II.

The data on langur diet were pooled into four seasons, according to the climatic pattern (see Chapter II); *i.e.*, the spring was in March, the summer between April and August, the autumn between September and November, and the winter between December and February. The pooled data were then analysed to indicate the seasonality of langur diet.

Home range size of each group was estimated using data collected from the study groups (see Section 4.3.1). Furuichi's formula (see above) was used to do a further comparison between the observed home range size and the expected home range size, so as to predict the possibility of living space for additional langur groups. Because all parts of GA8's home range were visibly accessible, data on group size and habitat quality from this group were used to estimate the constant $\alpha$ as follows.

$$\alpha = \mathbf{RQ/N,}$$

where R was the home range size, Q the habitat quality, and N the group size.

Correlation between variables was tested using the Pearson Product Moment Correlation Coefficient and the Spearman Rank Correlation Coefficient tests. The Kruskal-Wallis test was used to analyse the seasonality. Goodness of fit tests were used to compare the observed home range sizes and the predicted home range sizes calculated from Furuichi's formula. The Mann-Whitney U test, Wilcoxon test for matched pairs, and Discriminant Analysis were used to test differences between samples (Siegel & Castellan, 1988; Fowler & Cohen, 1992). Statistical analyses were done using SPSS for Windows™ Release 6.1, Minitab® for Windows Release 12.1, and Microsoft Excel 97.

There are two traditions of comparative biology (Redley, 1983). In one tradition, researchers (*e.g.*, ecologists) explore correlations between variables using data from all species available and these species are regarded as independent from each other. In statistics, this approach may have overestimated the true number of degrees of freedom, because these species are not indeed independent from each other due to their characters coming from their common ancestries (Harvey & Pagel, 1991). In biology, some correlations exist in different phylogenetic lines, but they may not be significant if data from species these lines are used. For example, there is close relationship between body size and diet, which is reflected in the difference between macaques and colobine monkeys. However, the frugivorous chimpanzees are much larger than the folivorous colobine monkeys in body size. When data from chimpanzees and colobine monkeys are used to test association between body size and folivory, the association may not be significant. This may be the reason why some obvious relationships are not significant.

In the other tradition, researchers (*e.g.*, taxonomists) make their comparisons on the basis of their common ancestry, which forms the obvious unifying principle. Harvey & Pagel (1991) suggested to bring these two types of comparative biology together, which seems to be an effective way to clarify some association that is obvious but not significant. Let's take the above example again. Colobine monkeys eat more leaves than macaques and are larger in body size. The frugivorous chimpanzees are smaller than the folivorous gorillas. Both cases follow the positive association between the quantity of leaves and the body size. In this chapter, comparisons across species will be made on the basis of phylogenetic lines.

## 5.3 Results

### 5.3.1 Diet

There were 1,424 records of feeding activity. Fifty plant species were recorded as food (*Table 5- 1*). Of these records, there were 43 in which food plant species identity was not certain and 39 records in which the food items were not seen clearly. Thus there were 1381 feeding records on identified plant species (Appendix C) and 1385 feeding records on identified food items (Appendix D).

The number of food plant species increased with the number of feeding records; *i.e.*, the number of food plant species found increased with the time of fieldwork. *Figure 5-1* shows that (a) the point of levelling off was at the point of 387 records, thus a group's general diet contained about 40-45 food plant species. (b) More food plant species would be found with more observation, but the increase of the species number would be very gradual. Eleven species (Spp. 49-59) were found eaten in the later stages of the study (July 98) and there were only a few feeding records collected from them. Therefore, it is suggested that a relatively complete list of food plant species has been obtained from this study, although more plant species may be found as langur foods with more observation time.

### *5.3.1.1 Food plant species*

Of the 50 plant species (see *Table 5- 1*), there were 26 species (52% of the total species number) whose records accounted for over 1% of the total records in the diet, 13 species (26%) over 2%, and only 5 species (10%) over 5%. This indicates that the langurs had a diverse diet in terms of plant species. There were two staple species, *Pteroceltis tatarinowii* (Spp. 2) and *Ficus microcarpa* (Spp. 26), which provided a large proportion of the total diet. Eight species (16% of the total food plant species) were among the 20 most common species in the habitat (accounting for 40% of the common species)(*Table 2- 6* and *Table 5- 2*). In terms of the P-index, these eight species were not highly preferred food species. There were 12 species in the diet that were not encountered during the vegetation composition analysis (Chapter II). They were excluded, and then all other species were scored according to the percentage of feeding records (*i.e.*, %(F) in *Table 5- 1*). The top fifteen species were selected for testing the association between %(F) and %(V), so as to measure if langur food selection was influenced by the frequency of occurrence of the plant species in the environment. Results showed that there was no significant correlation between the two variables (the Spearman Rank Correlation Coefficient $r_s = -0.1625$, two-tailed,

Table 5- 1 Food plant species list, arranged according to number of feeding records

| Species (code) | Family | Feeding records | %(F)* | %(V)* | P-index** |
|---|---|---|---|---|---|
| *Ficus microcarpa (26)* | MORACEAE | 221 | 16.0 | 0.09 | 177.81 |
| *Pteroceltis tatarinowii (2)* | ULMACEAE | 155 | 11.2 | 5.8 | 1.94 |
| *Capparis viminea (1)* | CAPPARIDACEAE | 128 | 9.3 | 0.1 | 92.69 |
| *Celtis sinensis (35)* | ULMACEAE | 80 | 5.8 | 0.3 | 19.31 |
| *Tetraceae asiatica (32)* | DILLENIACEAE | 78 | 5.6 | 0.04 | 141.20 |
| *Lindera communis (20)* | LAURACEAE | 68 | 4.9 | 3.16 | 1.56 |
| *Celtis austro-sinensis (5)* | ULMACEAE | 54 | 3.9 | 0.2 | 19.55 |
| *Broussonetia kazinoki (22)* | MORACEAE | 48 | 3.5 | 0.03 | 115.86 |
| *Cuscuta chinensis (24)* | CONVOLVULACEAE | 32 | 2.3 | no | |
| *Mappianthus iodoides (28)* | ICACINACEAE | 31 | 2.2 | 0.04 | 56.12 |
| *Millettia pachycarpa (29)* | PAPILIONACEAE | 31 | 2.2 | 1.06 | 2.12 |
| *Madhuca pasquieri (48)* | SAPOTACEAE | 30 | 2.2 | no | |
| *Sterculia euosma (41)* | STERCULIACEAE | 28 | 2.0 | 4.22 | 0.48 |
| *Pueraria thunbergiana (16)* | PAPILIONACEAE | 27 | 2.0 | 0.05 | 39.10 |
| *Pithecellobium clypearia (12)* | MIMOSACEAE | 27 | 2.0 | 0.38 | 5.15 |
| *Fluggea virosa (10)* | EUPHORBIACEAE | 25 | 1.8 | 4.5 | 0.40 |
| *Pistacia weinmannifolia (46)* | ANACARDIACEAE | 23 | 1.7 | 0.54 | 3.08 |
| *Ficus nervosa (13)* | MORACEAE | 22 | 1.6 | 0.04 | 39.83 |
| *Murraya paniculata (3)* | RUTACEAE | 22 | 1.6 | 0.8 | 1.99 |
| *Clausena excavata (21)* | RUTACEAE | 21 | 1.5 | 2.1 | 0.72 |
| *Jasminum albicalyx (31)* | OLEACEAE | 21 | 1.5 | no | |
| *Apodytes dimidiata (47)* | ICACINACEAE | 20 | 1.4 | no | |
| *Debregeasia edulis (45)* | URTICACEAE | 19 | 1.4 | 0.86 | 1.60 |
| *Sageretia hamosa (8)* | RHAMNACEAE | 17 | 1.2 | 0.02 | 61.55 |
| *Ficus altissima (37)* | MORACEAE | 15 | 1.1 | 0.03 | 36.21 |
| *Phyllanthus reticulata (49)* | EUPHORBIACEAE | 15 | 1.1 | 0.04 | 27.15 |
| *Litsea euosma (9)* | LAURACEAE | 13 | 0.9 | 3.4 | 0.28 |
| *Sageretia lucida (18)* | RHAMNACEAE | 12 | 0.9 | no | |
| *Cayratia japonica (25)* | VITACEAE | 11 | 0.8 | no | |
| *Caesalpinia sappan (51)* | CAESALPINIACEAE | 10 | 0.7 | 0.03 | 24.14 |
| *Breynia fruticosa (34)* | EUPHORBIACEAE | 8 | 0.6 | 0.02 | 28.96 |
| *Zenia insignis (17)* | CAESALPINIACEAE | 8 | 0.6 | 0.29 | 2.00 |
| *Cansjera rheedii (23)* | OPILIACEAE | 8 | 0.6 | 1.34 | 0.43 |
| *Cudrania cochinchinensis (6)* | MORACEAE | 8 | 0.6 | 3 | 0.19 |
| *Cryptolepis buchanani (11)* | ASCLEPIADACEAE | 7 | 0.5 | 0.02 | 25.34 |
| *Delavaya yunnanensis (56)* | SAPINDACEAE | 6 | 0.4 | 0.31 | 1.40 |
| *Iodes vitigina (55)* | ICACINACEAE | 5 | 0.4 | 0.001 | 362.06 |
| *Oroxylun indicum (4)* | BIGNONIACEAE | 5 | 0.4 | 5.9 | 0.06 |
| *Berchemia lineata (7)* | RHAMNACEAE | 5 | 0.4 | no | |
| *Vitex quinata (57)* | VERBENACEAE | 3 | 0.2 | 0.98 | 0.22 |
| *Gnetum montanum (44)* | GNETACEAE | 2 | 0.1 | 0.02 | 7.24 |
| *Toona sureni (27)* | MELIACEAE | 2 | 0.1 | 0.26 | 0.56 |
| *Pueraria montana (53)* | PAPILIONACEAE | 2 | 0.1 | no | |
| *Tinospora sinensis (58)* | MENISPERMACEAE | 2 | 0.1 | no | |
| *Morus australis (14)* | MORACEAE | 1 | 0.1 | 0.21 | 0.34 |
| *Ficus gibbosa (50)* | MORACEAE | 1 | 0.1 | 1.39 | 0.05 |
| *Lonicera japonica (15)* | CAPRIFOLIACEAE | 1 | 0.1 | no | |
| *Argyreia acuta (52)* | CONVOLVULACEAE | 1 | 0.1 | no | |
| *Argyreia capitata (54)* | CONVOLVULACEAE | 1 | 0.1 | no | |
| un-identified (59) | | 1 | 0.1 | | |
| Total | | 1381 | 100.0 | | |

* %(F) was percentage of the species' feeding records over the total feeding records, %(V) was the percentage of individuals of each species over the total number of individuals (data from Appendix A). ** The P-index was calculated using %(F) divided by %(V), and used to indicate the degree that a species was favoured by the langurs. Species were identified according to Guangxi Botanic Institute (1971) that followed Hutchinson's system, thus leguminous species were placed in the family Mimosaceae.

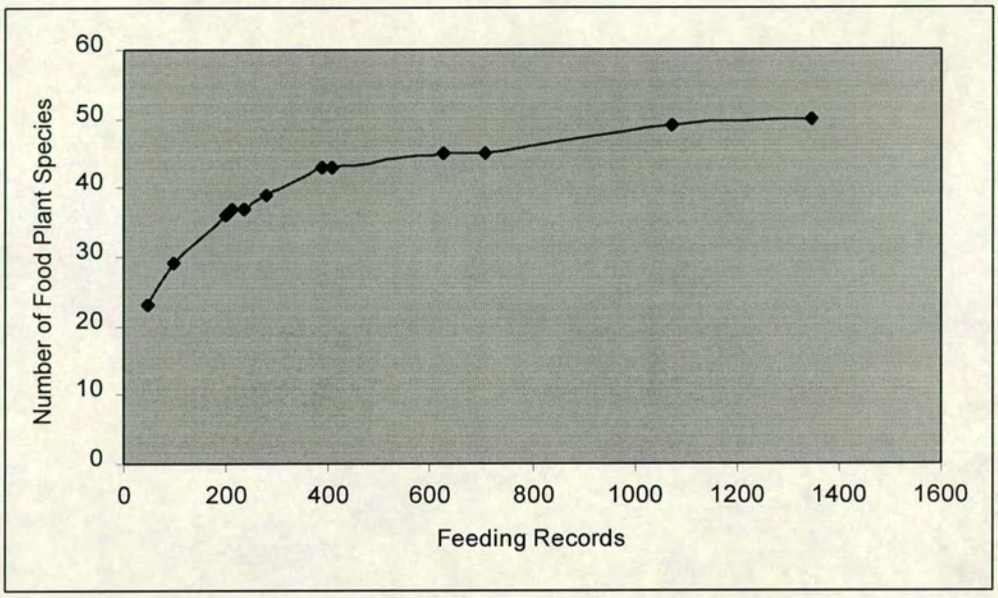


**Figure 5-1 Relationship between feeding records and the number of food plant species.**

p>0.05). This indicates that food selection was independent of the frequency of plant species in the habitat, and that white-headed langurs fed selectively only on some species. This is also supported by data in *Table 5- 2* in which most of the species had a low %(F).

**Table 5- 2 Common food plant species arranged according to frequency in the habitat (%V)**

| Species | Family | Feeding records | %(F)* | %(V)* | P-index |
|---|---|---|---|---|---|
| *Oroxylun indicum* | BIGNONIACEAE | 5 | 0.4 | 5.9 | 0.06 |
| *Pteroceltis tatarinowii* | ULMACEAE | 155 | 11.2 | 5.8 | 1.94 |
| *Fluggea virosa* | EUPHORBIACEAE | 25 | 1.8 | 4.5 | 0.40 |
| *Sterculia euosma* | STERCULIACEAE | 28 | 2.0 | 4.2 | 0.48 |
| *Litsea euosma* | LAURACEAE | 13 | 0.9 | 3.4 | 0.28 |
| *Lindera communis* | LAURACEAE | 68 | 4.9 | 3.2 | 1.56 |
| *Cudrania cochinchinensis* | MORACEAE | 8 | 0.6 | 3.0 | 0.19 |
| *Clausena excavata* | RUTACEAE | 21 | 1.5 | 2.1 | 0.72 |

It was shown by the number of common species in the list of food plant species and the P-index in *Table 5- 2* that white-headed langurs in general fed on less common species, rather than those plant species that were easily found. None of the 16 highly preferred species in the diet was among the 20 most common species in the habitat (*Table 2- 6*).

The 49 identified species belonged to 28 families (*Table 5- 3*). The ratio of species/family was 1.75. Feeding records for three families (Capparidaceae, Moraceae, and Ulmaceae) accounted for 53.1% of the total records, thus they were staple families. It should be pointed out that these families were also highly preferred, because they had more highly preferred species than other families.

### *5.3.1.2 Species diversity of Food plants*

The number of food plant species in the diet varied between different langur groups (*Table 5- 4*). To test the differences in food plant species diversity among groups, a comparison was made among GA3, GA4, and GA8 (*Table 5- 5*), because their feeding records accounted for a large proportion (63%) of the total feeding records.

Table 5-3 Alphabetical list of families to which food plant species belonged.

| Family | Feeding records | %(F) | %(V)* | No. HPS** |
|---|---|---|---|---|
| ANACARDIACEAE | 23 | 1.7 | 0.54 | 0 |
| ASCLEPIADACEAE | 7 | 0.5 | 0.02 | 1 |
| BIGNONIACEAE | 5 | 0.4 | 5.9 | 0 |
| CAESALPINIACEAE | 18 | 1.3 | 0.32 | 1 |
| CAPPARIDACEAE | 128 | 9.3 | 0.1 | 1 |
| CAPRIFOLIACEAE | 1 | 0.1 | no | |
| CONVOLVULACEAE | 34 | 2.5 | no | |
| DILLENIACEAE | 78 | 5.6 | 0.04 | 1 |
| EUPHORBIACEAE | 48 | 3.5 | 4.56 | 2 |
| GNETACEAE | 2 | 0.1 | 0.02 | 0 |
| ICACINACEAE | 56 | 4.1 | - | 2 |
| LAURACEAE | 81 | 5.9 | 6.56 | 0 |
| MELIACEAE | 2 | 0.1 | 0.26 | 0 |
| MENISPERMACEAE | 2 | 0.1 | no | |
| MIMOSACEAE | 27 | 2.0 | 0.38 | 0 |
| MORACEAE | 316 | 22.9 | 4.79 | 4 |
| OLEACEAE | 21 | 1.5 | no | |
| OPILIACEAE | 8 | 0.6 | 1.34 | 0 |
| PAPILIONACEAE | 60 | 4.3 | - | 1 |
| RHAMNACEAE | 34 | 2.5 | - | 1 |
| RUTACEAE | 43 | 3.1 | 2.9 | 0 |
| SAPINDACEAE | 6 | 0.4 | 0.31 | 0 |
| SAPOTACEAE | 30 | 2.2 | no | |
| STERCULIACEAE | 28 | 2.0 | 4.22 | 0 |
| ULMACEAE | 289 | 20.9 | 6.3 | 2 |
| URTICACEAE | 19 | 1.4 | 0.86 | 0 |
| VERBENACEAE | 3 | 0.2 | 0.98 | 0 |
| VITACEAE | 11 | 0.8 | no | |

* Some species were not encountered during the sampling (Chapter 2), thus the %(V) could not be calculated for some families. – Some species in the families were encountered, but others not, so no data presented. For calculation of %(V), see Table 5-1. **HPS = highly preferred species.

Table 5-4 Food plant species eaten by each langur group

| Groups | Group size* | No species eaten | Feeding records | Diversity Indexes Simpson | Shannon-Weaver |
|---|---|---|---|---|---|
| | | | | Overall | Overall |
| GA1 | 3 | 18 | 47 | 12.77 | 2.69 |
| GA2 | 6 | 22 | 80 | 10.26 | 2.68 |
| GA3 | 15 | 40 | 365 | 14.39 | 3.09 |
| GA4 | 9 | 22 | 220 | 4.38 | 2.00 |
| GA4-A | 4 | 10 | 22 | 7.81 | 2.16 |
| GA4-B | 9 | 28 | 111 | 11.88 | 2.84 |
| GA5 | 7 | 13 | 51 | 8.36 | 2.30 |
| GA6 | 11 | 2 | 3 | 1.80 | 0.64 |
| GA7 | 12 | 27 | 102 | 9.78 | 2.80 |
| GA8 | 5 | 36 | 285 | 15.17 | 3.09 |
| GAGL | 4 | 7 | 10 | 6.25 | 1.89 |
| GALN | 10 | 11 | 23 | 9.28 | 2.31 |
| overall | | 50 | 1381 | 15.49 | 3.20 |

Group size values were obtained by averaging the max and min group counts (see Chapter 6).

Table 5-5 Staple food species and families of the langur groups

| Groups | Staple species (N1) | % records | % N | Staple families (F1) | % records | F2 | % F |
|---|---|---|---|---|---|---|---|
| GA3 | *Ficus microcarpa* | 10.96 | | ULMACEAE | 28.77 | | |
| | *Tetraceae asiatica* | 6.58 | | | | | |
| | *Celtis sinensis* | 10.68 | | | | | |
| | *Pteroceltis tatarinowii* | 16.16 | | MORACEAE | 18.36 | | |
| | *Capparis viminea* | 7.12 | | CAPPARIDACEAE | 7.12 | | |
| Total | | 51.50 | 12.50 | 3 | 54.25 | 24 | 12.50 |
| GA4 | *Ficus microcarpa* | 37.73 | | MORACEAE | 40.00 | | |
| | *Lindera communis* | 27.27 | | LAURACEAE | 27.73 | | |
| Total | | 65.00 | 9.09 | 2 | 67.73 | 14 | 14.29 |
| GA8 | *Capparis viminea* | 15.44 | | CAPPARIDACEAE | 15.44 | | |
| | *Pteroceltis tatarinowii* | 12.63 | | ICACINACEAE | 11.23 | | |
| | *Pithecellobium clypearia* | 5.26 | | MORACEAE | 11.93 | | |
| | *Tetraceae asiatica* | 5.96 | | ULMACEAE | 20.70 | | |
| | *Sterculia euosma* | 5.26 | | | | | |
| | *Apodytes dimidiata* | 5.96 | | | | | |
| Total | | 50.51 | 16.67 | 4 | 59.30 | 23 | 17.39 |

F1 = number of staple food plant families. F2 = total number of plant families in the diet of the group. % N = percentage of the number of staple species over the total number of plant species in the diet of the langur group. % F = percentage of F1 over F2.

It was shown that GA3 and GA8 had similar staple food plant species and families. The only obvious difference was that the species *Lindera communis* (family Lauraceae) accounted for a considerable part of the diet of GA4. This species was found only in swamp areas around seasonal ponds or in seasonally flooded areas. A patch was located in LY1, a valley that was in the core area of GA4. The fruits matured in the winter of 1997 and were favoured by the langurs. Thus, it is assumed that *Lindera communis* may be a favourite food for all langur groups. It was not found in the diet of other groups, because it did not occur in their home ranges. GA4 was observed only in the winter of 1997. It soon split into GA4-A and GA4-B after a group takeover. This may be the reason that GA4 apparently had only 2 staple food plant species, because only winter diet was recorded for this group.

Feeding records on each species were transformed into diversity indices (the Simpson Index and the Shannon-Weaver Index). Data on the Shannon-Weaver index were compared with langur group size, which showed a strong correlation between the two variables (Spearman Rank correlation coefficient $r_s = 0.829$, n=12, two-tailed, $p<0.01$). This correlation may indicate a sampling error; *i.e.*, feeding records increased with the number of individuals observed. A langur group with more individuals may feed on more plant species during a single scan than a group with fewer individuals. In other words, more feeding records are likely to contain more food plant species. Thus a further test was made between group size and feeding records using data from each langur group, which did not show a significant correlation (Spearman Rank Correlation Coefficient $r_s=0.325$, n = 12, two-tailed, $p>0.1$). These tests indicated that the fact that larger groups had a more diverse diet than small groups reflected differences in behaviour but was not a sampling error. Thus, it is suggested that white-headed langurs had a tendency to feed on as many plant species as possible.

### *5.3.1.3 Seasonal use of food plant species*

Plant species were not evenly used by langurs (*Table 5- 6*) throughout the year. According to the feeding records and the seasons, the 50 food plant species were

Table 5-6 Feeding records of the food plant species in different months (for species code, see Table 5-1)

| month | species | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 31 | 32 | 34 | 35 | 37 |
| 97.09. | | | | | | 1 | | | | | | 1 | | | | | 1 | | | | 5 | | | | | | | | | 1 | | 1 | |
| 97.10. | 2 | 2 | | | 2 | | | | | | | 2 | | | | 3 | 1 | | 1 | | | | 1 | 1 | 3 | | | 2 | | 1 | | 5 | |
| 97.11. | 4 | 5 | | | | | | | | | | | | | | | | | 41 | | 3 | | 3 | | 52 | | | | | 1 | 1 | 7 | |
| 97.12. | 5 | 9 | 1 | 2 | 3 | | | 3 | | | | | | | | 2 | | | 9 | 1 | 2 | | 10 | | 22 | | 1 | 6 | 2 | | 1 | 2 | |
| 98.01. | 6 | 4 | 6 | | 8 | 2 | 1 | 1 | | | | 1 | | | | | | 1 | | 2 | | 1 | 1 | | 19 | | 1 | 3 | 1 | 3 | | 1 | |
| 98.02. | 23 | 4 | 3 | | 7 | | 1 | 6 | 1 | | | 2 | | | 1 | 2 | | 3 | 17 | 6 | | 1 | 7 | | 38 | | 3 | 7 | 4 | 4 | 3 | | 2 |
| 98.03. | 13 | 19 | | | 3 | 2 | 1 | 3 | | 6 | | 1 | 11 | 1 | | | 1 | | | 3 | 7 | | 3 | | 20 | | 1 | 2 | 4 | 17 | | | |
| 98.04. | 10 | 27 | 1 | | 4 | | | 2 | 3 | 3 | | 7 | 3 | | | 1 | | 1 | | 2 | 3 | 1 | | | 12 | | | 1 | 2 | 24 | 2 | 19 | 2 |
| 98.05. | 27 | 22 | 4 | 2 | 8 | 1 | 2 | 2 | 2 | 4 | | 9 | 4 | | | 6 | 5 | 2 | | 4 | 7 | 1 | 2 | 1 | 14 | 1 | 10 | 1 | 3 | 2 | | 19 | 1 |
| 98.06. | 14 | 11 | | | 6 | | | | 1 | 5 | 4 | | 1 | | | 3 | | 2 | | 1 | 7 | 1 | 3 | 4 | 2 | 1 | 7 | 1 | 1 | 12 | | 3 | 1 |
| 98.07. | 8 | 17 | 4 | | 4 | | | | 5 | 2 | | | 1 | | | 3 | | 2 | | 1 | 5 | | | | 24 | | | 4 | 1 | 2 | 1 | 6 | 6 |
| 98.08. | 9 | 17 | 2 | | 6 | 2 | | | | 5 | 1 | 3 | 1 | | | 1 | | 1 | | 1 | 3 | 2 | 1 | 3 | 6 | | 5 | 4 | 2 | 7 | | 11 | 3 |
| 98.09. | 7 | 18 | 1 | 1 | 3 | | | | 1 | | 2 | 1 | 1 | | | 6 | | | | | 6 | 1 | 1 | 2 | 9 | | 3 | | 1 | 4 | | 6 | |
| total | 128 | 155 | 22 | 5 | 54 | 8 | 5 | 17 | 13 | 25 | 7 | 27 | 22 | 1 | 1 | 27 | 8 | 12 | 68 | 21 | 48 | 8 | 32 | 11 | 221 | 2 | 31 | 31 | 21 | 78 | 8 | 80 | 15 |
| % | 9 | 11 | 1.5 | 0.4 | 3.8 | 0.6 | 0.4 | 1.2 | 0.9 | 1.8 | 0.5 | 1.9 | 1.5 | 0.1 | 0.1 | 1.9 | 0.6 | 0.8 | 4.8 | 1.5 | 3.4 | 0.6 | 2.2 | 0.8 | 16 | 0.1 | 2.2 | 2.2 | 1.5 | 5.5 | 0.6 | 5.6 | 1.1 |

| | 41 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | unk |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 97.09. | | | | | | | | | | | | | | | | | | 2 |
| 97.10. | | | | | | | | | | | | | | | | | | 7 |
| 97.11. | | | | | | | | | | | | | | | | | | 5 |
| 97.12. | | | | | | | | | | | | | | | | | | 9 |
| 98.01. | | | | | | | | | | | | | | | | | | 6 |
| 98.02. | | 1 | 1 | | | | | | | | | | | | | | | 2 |
| 98.03. | 3 | | 6 | 3 | | | | | | | | | | | | | | 10 |
| 98.04. | 6 | | 1 | 10 | 16 | | | | | | | | | | | | | 2 |
| 98.05. | 1 | 1 | 1 | 3 | | | | | | | | | | | | | | |
| 98.06. | 6 | | | 1 | | 2 | | | | | | | | | | | | |
| 98.07. | 8 | | 1 | 2 | | 2 | 3 | 1 | | | | | | | | | | |
| 98.08. | 1 | | 3 | 2 | 3 | 18 | 10 | | 4 | | 1 | 1 | 3 | 1 | | | | |
| 98.09. | 3 | | 6 | 2 | 1 | 8 | 2 | | 6 | 1 | 1 | | 2 | 5 | 3 | 2 | 1 | |
| total | 28 | 2 | 19 | 23 | 20 | 30 | 15 | 1 | 10 | 1 | 2 | 1 | 5 | 6 | 3 | 2 | 1 | 43 |
| % | 2 | 0.1 | 1.3 | 1.6 | 1.4 | 2.1 | 1.1 | 0.1 | 0.7 | 0.1 | 0.1 | 0.1 | 0.4 | 0.4 | 0.2 | 0.1 | 0.1 | 3 |

classified into *year-round* (16 species) and *seasonal foods* (19 species)(*Table 5- 7*). Of the 16 year-round species, some were eaten more in some seasons than in others. There were 15 species that were eaten very rarely and 11 of them (Spp. 49-59) were eaten only in the final stage of the fieldwork.

Because of their similarity, data from GA3 and GA8 were combined together, and used to indicate the seasonal changes in the use of food plant species by white-headed langurs (*Table 5- 8*). In the diet of these two groups, some species (*i.e.*, *Capparis viminea*, *Pteroceltis tatarinowii,* and *Tetraceae asiatica*) were staple food plant species in almost every month, while others changed their role in different months. Only one leguminous species, *Pithecellobium clypearia,* was present in the langur diet. This species was not used as a staple species between December 1997 and March 1998 and was present in the staple species list only once in May 1998. Species used in the lean season between December 1997 and February 1998 provided keystone plant resources (Terborgh, 1986) and are regarded as keystone species, including *C. viminea*, *Cuscuta chinensis, Murraya paniculata, P. tatarinowii, Sageretia hamosa,* and *T. asiatica.*

There was no difference in the identity of staple food plant species between langur groups. Further tests using data collected from GA3 and GA8 from November 97 to September 98 showed that these two langur groups did not differ significantly in the seasonality of food plant species diversity (Mann-Whitney test $U = 40.0$, $n_1 = 9$, $n_2 = 11$, $p > 0.05$). It was therefore assumed that there would be no significant differences between any of the other groups, and so all data were pooled. *Figure 5- 2* shows food plant species diversity from September 1997 to September 1998. It did not show any evidence of significant seasonal change (the Kruskal-Wallis test $K = 20.27$, $df = 12$, $p > 0.05$). This fact was also supported by a strong correlation (Spearman Rank Correlation Coefficient $r_S = 0.791$, $n=10$, two-tailed, $p<0.01$) between diet diversity and feeding activity which was previously shown to be relatively even all year (Chapter IV).

Table 5-7 Summary of seasonality of food plant species use

| Types | Species Code | Species | Family | Comments |
|---|---|---|---|---|
| Year-round: | 1 | *Capparis viminea* | CAPPARIDACEAE | heavily used from Feb. to Jun. |
| | 2 | *Pteroceltis tatarinowii* | ULMACEAE | heavily used from Mar. to Sept.. |
| | 3 | *Murraya paniculata* | RUTACEAE | randomly |
| | 5 | *Celtis austro-sinensis* | ULMACEAE | evenly used in time |
| | 6 | *Cudrania cochinchinensis* | MORACEAE | randomly |
| | 12 | *Pithecellobium clypearia* | MIMOSACEAE | randomly |
| | 16 | *Pueraria thunbergiana* | PAPILIONACEAE | evenly used in time |
| | 22 | *Broussonetia kazinoki* | MORACEAE | evenly used in time |
| | 23 | *Cansjera rheedii* | OPILIACEAE | evenly from Jan. to Sept. |
| | 24 | *Cuscuta chinensis* | CONVOLVULACEAE | heavily used in Dec. |
| | 26 | *Ficus microcarpa* | MORACEAE | heavily used from Nov. to Mar. |
| | 29 | *Millettia pachycarpa* | PAPILIONACEAE | evenly used in time |
| | 31 | *Jasminum albicalyx* | OLEACEAE | evenly used from Dec. to Sept. |
| | 32 | *Tetraceae asiatica* | DILLENIACEAE | heavily used in Mar. & Apr. |
| | 34 | *Breynia fruticosa* | EUPHORBIACEAE | evenly used |
| | 35 | *Celtis sinensis* | ULMACEAE | heavily used in Apr. & May |
| Seasonal: | 7 | *Berchemia lineata* | RHAMNACEAE | from Jan. to Mar. |
| | 8 | *Sageretia hamosa* | RHAMNACEAE | from Dec. to May |
| | 9 | *Litsea euosma* | LAURACEAE | from Apr. to Jul. |
| | 10 | *Fluggea virosa* | EUPHORBIACEAE | from Mar. to Aug. |
| | 11 | *Cryptolepis buchanani* | ASCLEPIADACEAE | from Jun. to Sept. |
| | 13 | *Ficus nervosa* | MORACEAE | more from Mar. to May |
| | 17 | *Zenia insignis* | CAESALPINIACEAE | more in May |
| | 18 | *Sageretia lucida* | RHAMNACEAE | from Jan. to Aug. |
| | 20 | *Lindera communis* | LAURACEAE | from Nov. to Feb. |
| | 21 | *Clausena excavata* | RUTACEAE | from Dec. to Aug. |
| | 25 | *Cayratia japonica* | VITACEAE | more in June |
| | 28 | *Mappianthus iodoides* | ICACINACEAE | more in May & Jun. |
| | 37 | *Ficus altissima* | MORACEAE | from Apr. to Aug. |
| | 41 | *Sterculia euosma* | STERCULIACEAE | from Mar. to Sept. |
| | 45 | *Debregeasia edulis* | URTICACEAE | from Feb. to Sept. |
| | 46 | *Pistacia weinmannifolia* | ANACARDIACEAE | in Apr. |
| | 47 | *Apodytes dimidiata* | ICACINACEAE | in Apr. |
| | 48 | *Madhuca pasquieri* | SAPOTACEAE | in Aug. |
| | 49 | *Phyllanthus reticulata* | EUPHORBIACEAE | in Aug. |
| Rare* | 4 | *Oroxylun indicum* | BIGNONIACEAE | |
| | 14 | *Meras australis* | MORACEAE | |
| | 15 | *Lonicera japonica* | CAPRIFOLIACEAE | |
| | 27 | *Toona sureni* | MELIACEAE | |
| | 44 | *Gnetum montanum* | GNETACEAE | |
| | 50 | *Ficus gibbosa* | MORACEAE | |
| | 51 | *Caesalpinia sappan* | CAESALPINIACEAE | |
| | 52 | *Argyreia acuta* | CONVOLVULACEAE | |
| | 53 | *Pueraria montana* | PAPILIONACEAE | |
| | 54 | *Argyreia capitata* | CONVOLVULACEAE | |
| | 55 | *Iodes vitigina* | ICACINACEAE | |
| | 56 | *Delavaya yunnanensis* | SAPINDACEAE | |
| | 57 | *Vitex quinata* | VERBENACEAE | |
| | 58 | *Tinospora sinensis* | MENISPERMACEAE | |
| | 59 | un-identified | | |

* Rare species were eaten so rarely by langurs that it was difficult to determine if they were seasonally used or used year-round.

Table 5-8 Staple food plant species in each month for groups GA3 & GA8

| Months | N1 | N2 | % | Staple species | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 97.12. | 7 | 3 | 42.9 | *C. viminea* | *C. chinensis* | *P. tatarinowii* | | | | | |
| | | | | 18.2 | 18.2 | 36.4 | | | | | |
| 98.01. | 6 | 2 | 33.3 | *M. paniculata* | *T. asiatica* | | | | | | |
| | | | | 40.0 | 20.0 | | | | | | |
| 98.02. | 13 | 3 | 23.1 | *C. viminea* | *P. tatarinowii* | *S. hamosa* | | | | | |
| | | | | 29.4 | 11.8 | 11.8 | | | | | |
| 98.03. | 17 | 4 | 23.5 | *C. viminea* | *F. microcarpa* | *F. nervosa* | *P. tatarinowii* | | | | |
| | | | | 15.0 | 10.0 | 18.3 | 13.3 | | | | |
| 98.04. | 23 | 4 | 17.4 | *A. dimidiata* | *C. sinensis* | *P. tatarinowii* | *T. asiatica* | | | | |
| | | | | 11.7 | 12.5 | 18.0 | 11.7 | | | | |
| 98.05. | 20 | 4 | 20.0 | *C. viminea* | *C. sinensis* | *P. clypearia* | *P. tatarinowii* | | | | |
| | | | | 18.2 | 10.2 | 10.2 | 15.9 | | | | |
| 98.06. | 19 | 5 | 26.3 | *B. kazinoki* | *C. viminea* | *M. iodoides* | *S. euosma* | *T. asiatica* | | | |
| | | | | 9.3 | 13.0 | 9.3 | 11.1 | 13.0 | | | |
| 98.07. | 19 | 4 | 21.1 | *C. sinensis* | *F. altissima* | *F. microcarpa* | *P. tatarinowii* | | | | |
| | | | | 9.1 | 9.1 | 25.8 | 13.6 | | | | |
| 98.08. | 26 | 6 | 23.1 | *C. sinensis* | *C. cochinchinensis* | *M. pasquieri* | *P. reticulata* | *P. tatarinowii* | *T. asiatica* | | |
| | | | | 10.2 | 6.1 | 11.2 | 8.2 | 8.2 | 6.1 | | |
| 98.09. | 27 | 8 | 29.6 | *B. kazinoki* | *C. sappan* | *C. viminea* | *C. sinensis* | *D. edulis* | *F. microcarpa* | *M. pasquieri* | *P. tatarinowii* |
| | | | | 6.7 | 6.7 | 5.6 | 5.6 | 5.6 | 7.9 | 5.6 | 18.0 |

N1 = total number of food plant species; N2 = number of staple food plant specie. % is the percentage of N2 over N1. Figures under each species are the percentages of the feeding records on the species over the total records.

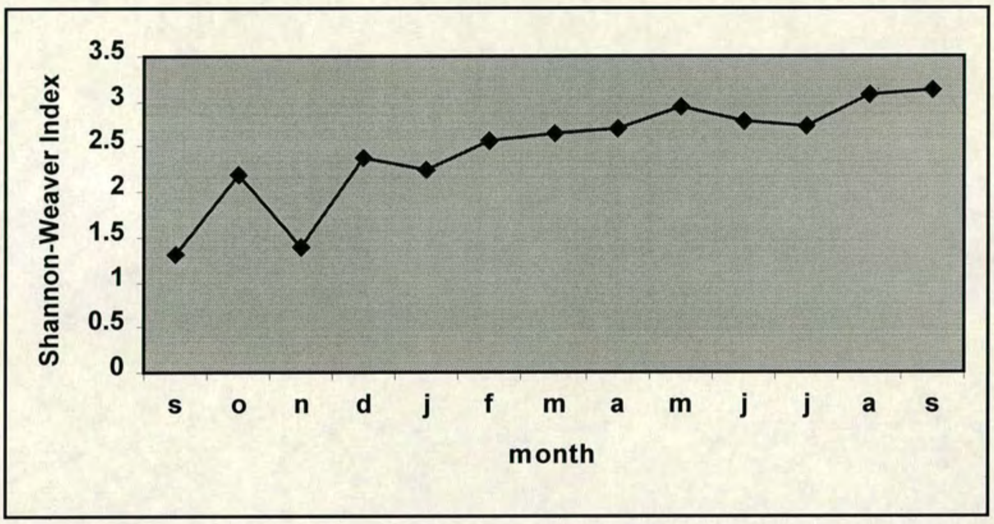


**Figure 5- 2 Changes in the diversity of food plant species for all langur groups between September 1997 and September 1998.**

#### *5.3.1.4 Food items*

Of the 1385 records of feeding items (Appendix D), leaves accounted for 91.4% of the total feeding records, flowers 1.4%, fruit 5.3%, and seeds 0.3%. The stem of *Cuscuta chinensis* (Family Convolvulaceae) accounted for 1.6% of the feeding records. *Table 5- 9* shows overall annual langur diet.

Leaves were obviously the staple food item of langurs. Among leaf categories, young leaves played the most important role in the langur diet (accounting for 79.1% of the total records). The P-index showed that langurs strongly preferred young leaves (P-index = 10.69), but not mature leaves (P-index = 0.09). Data from GA3 and GA8 were selected for a comparison with phenological data (Chapter II), which did not show any significant correlation between food availability and the proportion of feeding records for young and mature leaves (Pearson Correlation $R = 0.584$, $p > 0.05$ for young leaf, and $R = -0.109$, $p > 0.10$ for mature leaf). This indicates that the leaf-eating of langurs was not opportunistic.

Flowers, fruits, and seeds accounted for a relatively small part of the langur diet, but fruits seemed to be a favourite food item. This will be discussed further later.

#### *5.3.1.5 Food items in the diet of different langur groups*

It was shown in *Table 5- 9* that the diet of different groups varied. The difference in diet may be related to differences in the home range locality of the langur groups. *Lindera communis* (Family Lauraceae) grew in clumps around seasonal ponds. Six big clumps were found; each was respectively in the valley LGQ, LL, LY1, LY2, LY3, and LGT. The clumps in LGQ and LL were not in the feeding sites of any study groups. *L. communis* in LY2 and LY3 did not grow fruits in 1997-1998. Due to the dense canopy in LGT, no observations were conducted in that valley. LY1 was the core area of GA4. Because of the excellent observation conditions, large amounts of time were spent observing the group in the valley between November 1997 and February 1998. The maturing season of fruits was between November and December during which the langur group fed heavily on them. 50 records were collected for feeding on this plant species, in all of which the langurs ate the mature fruits. Mature

Table 5-9 Proportions of food items in the diet of different langur groups

| Groups | YL | ML | SL | L | FLBD | OPFL | FL | IMFR | MFR | ST | Seed |
|---|---|---|---|---|---|---|---|---|---|---|---|
| GA1 | 0.778 | 0.111 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.022 | 0.044 | 0.044 | 0.000 |
| GA2 | 0.878 | 0.085 | 0.012 | 0.012 | 0.000 | 0.000 | 0.000 | 0.012 | 0.000 | 0.000 | 0.000 |
| GA3 | 0.759 | 0.081 | 0.000 | 0.092 | 0.022 | 0.003 | 0.003 | 0.011 | 0.000 | 0.011 | 0.019 |
| GA4 | 0.581 | 0.108 | 0.000 | 0.000 | 0.045 | 0.000 | 0.000 | 0.000 | 0.225 | 0.041 | 0.000 |
| GA4' | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| GA4" | 0.775 | 0.045 | 0.000 | 0.054 | 0.000 | 0.000 | 0.009 | 0.036 | 0.054 | 0.018 | 0.009 |
| GA5 | 0.712 | 0.231 | 0.000 | 0.019 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.038 | 0.000 |
| GA6 | 0.667 | 0.000 | 0.000 | 0.333 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| GA7 | 0.804 | 0.049 | 0.000 | 0.039 | 0.069 | 0.000 | 0.000 | 0.020 | 0.000 | 0.020 | 0.000 |
| GA8 | 0.778 | 0.077 | 0.000 | 0.025 | 0.007 | 0.007 | 0.000 | 0.070 | 0.004 | 0.025 | 0.007 |
| GAGL | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| GALN | 0.762 | 0.000 | 0.000 | 0.095 | 0.000 | 0.000 | 0.000 | 0.000 | 0.143 | 0.000 | 0.000 |
| Mean | 0.791 | 0.066 | 0.001 | 0.056 | 0.012 | 0.001 | 0.001 | 0.014 | 0.039 | 0.016 | 0.003 |
| S.E. | 0.035 | 0.019 | 0.001 | 0.027 | 0.006 | 0.001 | 0.001 | 0.006 | 0.021 | 0.005 | 0.002 |

Abbreviations: YL, young leaves; ML, mature leaves; SL, senescing leaves; L, leaves (photo-phases not clear); FLBD, flower buds; OPFL, open flowers; FL, flower buds + open flowers; IMFR, immature fruit; MFR, mature fruit; ST, stem of vine.

fruits of *L. communis* accounted for as high as 39.8% of the feeding records in November, 36% in December, and 22.5% in the overall diet of GA4. The P-index was 99.5 (39.8/0.4) in November. All fruits disappeared from the tagged *L. communis* individuals in December, thus there were no data on the availability of mature fruits, so a P-index could not be calculated for that month.

Mature fruits of *Ficus microcarpa* (Family Moraceae) accounted for 14.3% of the diet of the group GALN. Seeds of *Caesalpinia sappan* (Family Caesalpiniaceae) made up 1.9% of the 7 records of seed eating in the diet of group GA3. These records were made in the valley LG, an important feeding site of this langur group, where *C. sappan* was first recorded as a food plant species. These two plant species were mainly found on cliffs, thus only a few individuals were encountered in the vegetation survey. So no further analysis could be made. *Table 5- 10* shows a summary of food plant species and food items.

Data on food items were compared among all langur groups using discriminant analysis. The results showed that these groups did not differ significantly from one another ($p>0.1$), which indicates that they had broadly similar diets. However, YL and ML played an important part in discriminating these groups (discriminant function coefficient of YL in Function 1 was 1.25, and that of ML was 1.21). This means that leaves (young and mature) were the staple part of the diets of these langur groups. A comparison with other *Presbytis* species (*Table 5- 11*) showed that the white-headed langur was extremely folivorous. Compared to other colobine study sites in Asia (see Section 2.4.3), young leaves were less in Bapen, which suggests that a diet containing a large proportion of young leaves may be the preferred diet of white-headed langurs, rather than the outcome of habitat constraints.

#### *5.3.1.6 Seasonal changes in food items*

Because there were no significant differences in diet among the 12 langur groups, data from them were pooled together for analysing seasonality of food items and are shown in *Figure 5- 3*. It is shown here that a high level of young leaves was maintained in the diet almost year-round. In the winter (from December 1997 to January 1998), both monthly rainfall and the availability of young leaves dropped

Table 5-10 Food items from different food plant species (% of feeding records on the species over the overall records for the item. For abbreviations, see Table 5-9)

| Species | Items | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | YL | ML | L | FLBD | OPFL | FL | IMFR | MFR | ST | Seeds |
| *Ficus microcarpa* | 18.42 | 10.71 | 14.52 | | | | | 11.67 | | |
| *Pteroceltis tatarinowii* | 11.43 | 12.50 | 35.48 | | | | | | | |
| *Capparis viminea* | 11.33 | 10.71 | 1.61 | | | | | | | |
| *Tetraceae asiatica* | 7.19 | 2.68 | | | | | | | | |
| *Celtis sinensis* | 6.50 | 5.36 | 11.29 | | | | | | | |
| *Celtis austro-sinensis* | 4.14 | 7.14 | 4.84 | | | | | | | |
| *Broussonetia kazinoki* | 3.05 | 9.82 | 3.23 | | | | | | | |
| *Madhuca pasquieri* | 2.86 | | | 3.57 | | | | | | |
| *Millettia pachycarpa* | 2.76 | 1.79 | | | | | | | | 9.09 |
| *Pueraria thunbergiana* | 2.46 | 0.89 | | 3.57 | | | | | | |
| *Fluggea virosa* | 2.36 | | 1.61 | | | | | | | |
| *Mappianthus iodoides* | 2.07 | 3.57 | 3.23 | | 33.33 | | 9.52 | | | |
| *Sterculia euosma* | 1.97 | 1.79 | | | | | 14.29 | | | 9.09 |
| *Pistacia weinmannifolia* | 1.97 | 2.68 | 1.61 | | | | | | | |
| *Ficus nervosa* | 1.87 | | | | | | 9.52 | | | |
| *Murraya paniculata* | 1.77 | 3.57 | | | | | | | | |
| *Pithecellobium clypearia* | 1.67 | 7.14 | | 3.57 | | | | | | |
| *Clausena excavata* | 1.48 | 2.68 | | 7.14 | | | | | | |
| *Phyllanthus reticulata* | 1.48 | | | | | | | | | |
| *Sageretia hamosa* | 1.38 | 2.68 | | | | | | | | |
| *Jasminum albicalyx* | 1.28 | 4.46 | 4.84 | | | | | | | |
| *Sageretia lucida* | 1.18 | | | | | | | | | |
| *Litsea euosma* | 0.99 | | | 3.57 | | | 4.76 | 1.67 | | |
| *Zenia insignis* | 0.79 | | | | | | | | | |
| *Cayratia japonica* | 0.79 | | 3.23 | | | | | | | |
| *Cansjera rheedii* | 0.69 | 0.89 | | | | | | | | |
| *Breynia fruticosa* | 0.69 | 0.89 | | | | | | | | |
| *Ficus altissima* | 0.59 | | 1.61 | | | | 33.33 | 1.67 | | |
| *Delavaya yunnanensis* | 0.59 | | | | | | | | | |
| *Cudrania cochinchinensis* | 0.49 | 1.79 | | | | | | | | |
| *Berchemia lineata* | 0.49 | | | | | | | | | |
| *Iodes vitigina* | 0.49 | | | | | | | | | |
| *Cryptolepis buchanani* | 0.39 | | 4.84 | | | | | | | |
| *Debregeasia edulis* | 0.39 | 0.89 | 8.06 | 21.43 | 33.33 | 100.00 | | | | |
| *Apodytes dimidiata* | 0.39 | | | | | | 28.57 | | | |
| *Oroxylun indicum* | 0.30 | 1.79 | | | | | | | | |
| *Vitex quinata* | 0.30 | | | | | | | | | |
| *Toona sureni* | 0.20 | | | | | | | | | |
| *Argyreia acuta* | 0.20 | | | | | | | | | |
| *Lonicera japonica* | 0.10 | | | | | | | | | |
| *Gnetum montanum* | 0.10 | 0.89 | | | | | | | | |
| *Caesalpinia sappan* | 0.10 | | | | | | | | | 81.82 |
| *Pueraria montana* | 0.10 | | | | | | | | 3.03 | |
| *Argyreia capitata* | 0.10 | | | | | | | | | |
| un-identified | 0.10 | | | | | | | | | |
| *Meras australis* | | | | | 33.33 | | | | | |
| *Lindera communis* | | 0.89 | | 57.14 | | | | 83.33 | | |
| *Cuscuta chinensis* | | | | | | | | | 96.97 | |
| *Ficus gibbosa* | | | | | | | | 1.67 | | |
| *Tinospora sinensis* | | 1.79 | | | | | | | | |

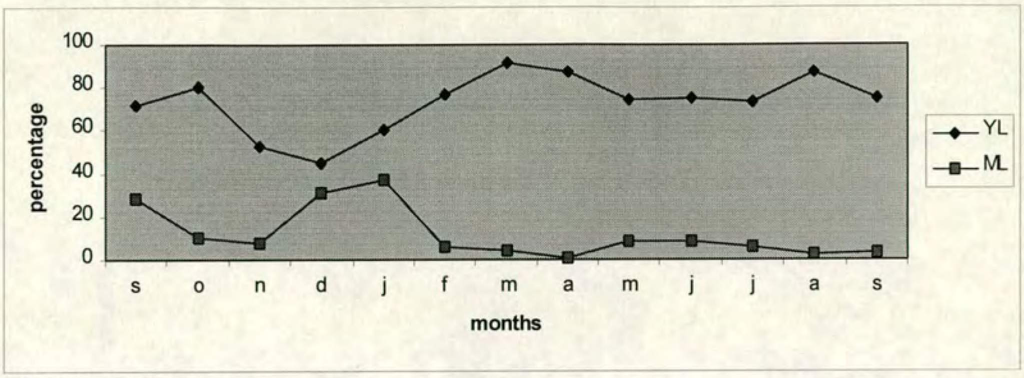
**Table 5- 11 Comparison of annual diets of *Presbytis* species**

| Species | Diets (% of feeding records) | | | |
|---|---|---|---|---|
| | Leaves | Fruit | Seeds | Source |
| *P. (P.) melalophos* | 32 | 50 | 20 | 1 |
| *P. (P.) potenziani* | 55 | 32 | | 2 |
| *P. (P.) rubicunda* | 40 | 20 | 30 | 3, 4 |
| *P. (S.) entellus* | 51.6 | 24.5 | | 5 |
| *P. (S.) entellus* | 50 | 45 | | 6 |
| *P. (T.) auratus* | 50 | 27~37 | | 7 |
| *P. (T.) auratus* | 55 | | | 8 |
| *P. (T.) johnii* | 60 | 28 | | 9 |
| *P. (T.) pileatus* | 57.8 | 24.4 | 9.3 | 10 |
| *P. (T.) vetulus* | 60 | 30 | | 6 |
| *P. (T.) leucocephalus* | 91.4 | 6.3 | 0.3 | present study |

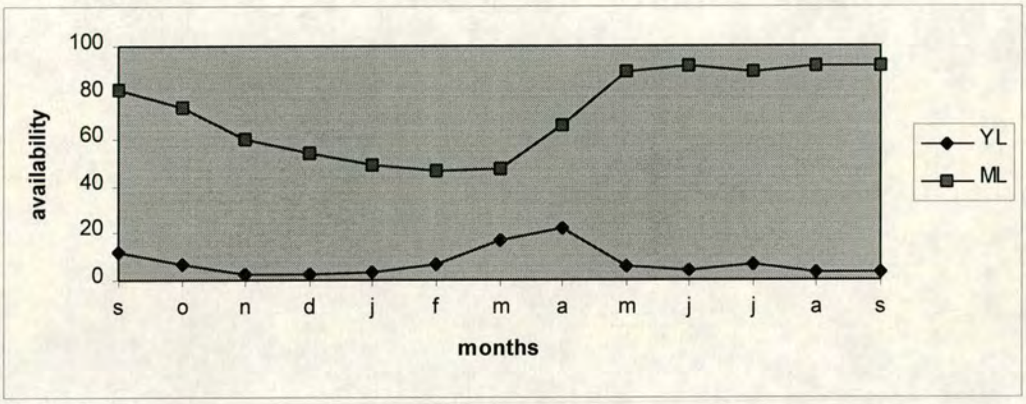
Source: 1. Bennett (1983), 2. Fuentes (1996), 3. Davies (1991), 4. Davies *et al.* (1988), 5. Newton (1992), 6. Hladik (1977), 7. Palmieri *et al.* (1984), 8. Kool (1989), 9. Oates *et al.* (1980), and 10. Stanford (1991).

showed that the amount of young leaves in the diet decreased between November nearly to zero (see *Figure 2- 6*b and *Figure 2- 13*). A comparison (*Figure 5- 3*) 1997 and January 1998 precisely according to the patterns of their availability in the environment. Thus there should be a positive correlation between young leaf availability and the amount in the diet, which was supported by the Spearman rank correlation coefficient test ($r_S = 0.76$, $n = 13$, one-tailed, $p < 0.005$). This may be because young leaves were preferred by langurs, but only a small amount was available year-round. Thus the feeding was dominated by the availability. During the same period, feeding on mature leaves increased and peaked. The amount of mature leaves in the diet was not influenced by availability (Spearman rank correlation coefficient $rs = 0.44$, $n = 13$, two-tailed, $p > 0.1$). Results of the Kruskal-Wallis test showed significant seasonality of use of young leaves by langurs from October 1997 to August 1998 ($K = 45.6$, $df = 10$, $p < 0.01$).

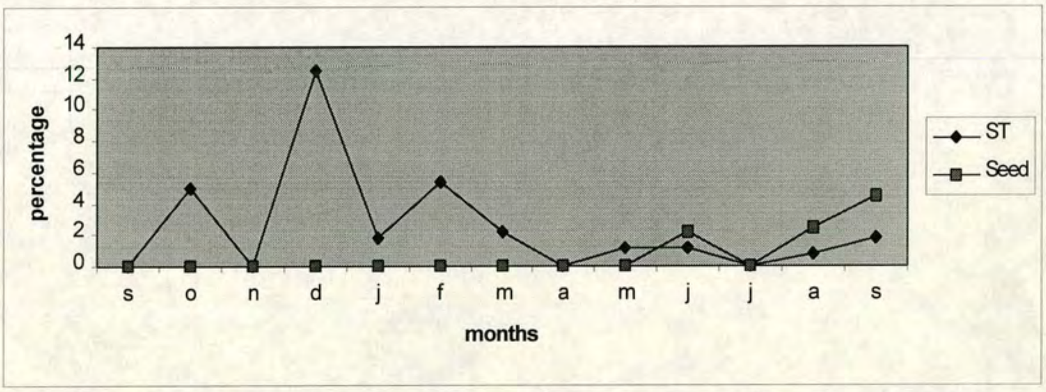
While young leaves became more and more difficult to get during the lean season between October 1997 and February 1998, other food items, including flowers, fruits, and stem (*Figure 5- 3*b, c, and d) reached high levels in the langur diet. Feeding on flower buds peaked in February 1998, but their availability



(a) Feeding

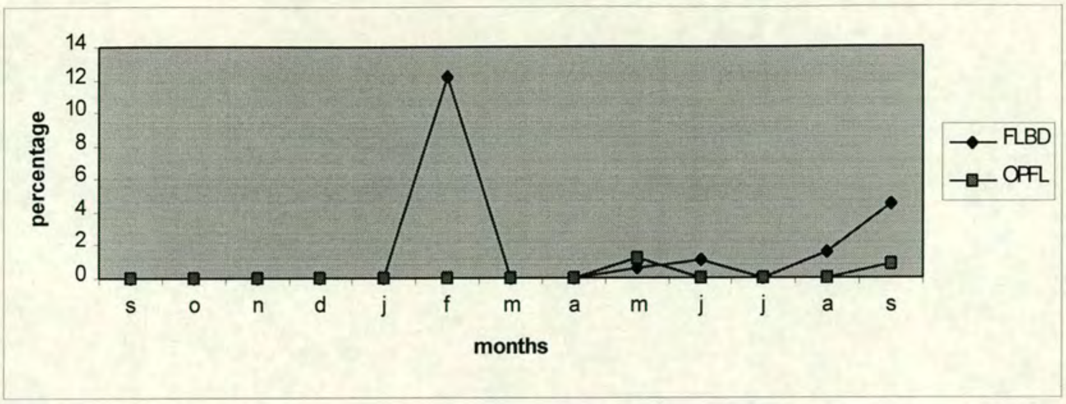


(b) Availability

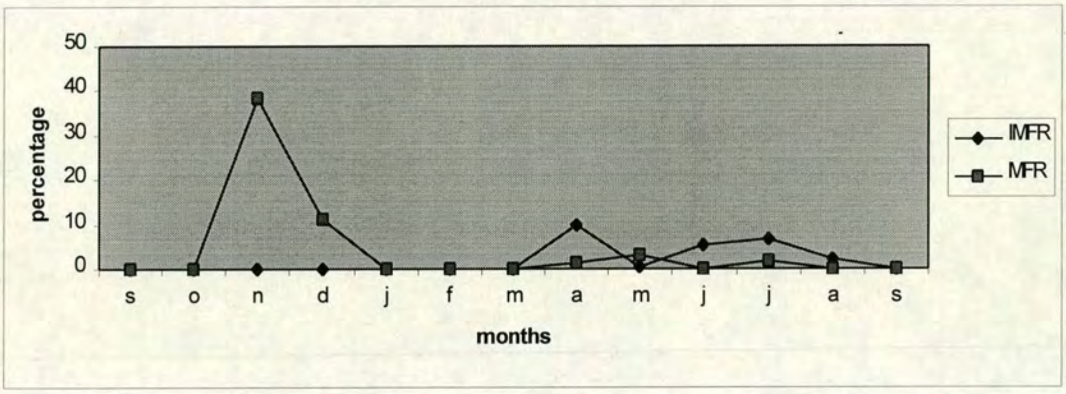


(c) Feeding

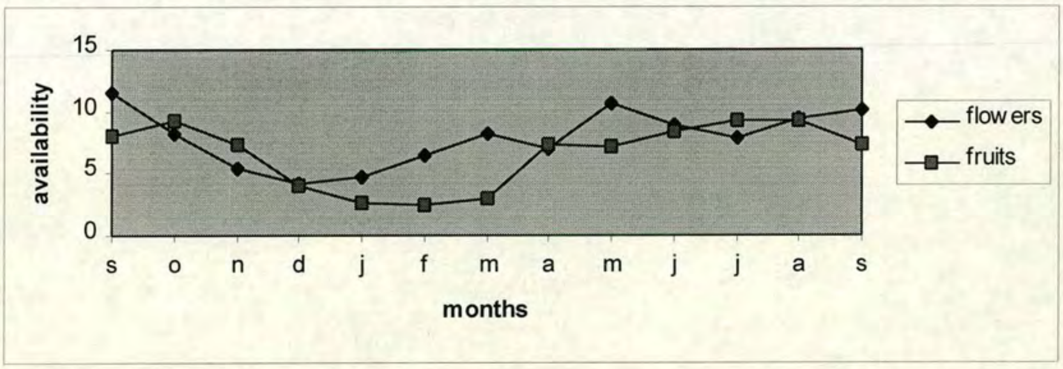
**Figure 5-3 (A) Seasonal changes in the use of food items. In the feeding charts, percentage on Axis Y was calculated using data of feeding records of a given food item divided by the total feeding records multiplied by 100%. In the availability chart, percentage on Axis Y was calculated using the actual scores divided by maximum potential scores. YL: young leaves, ML: mature leaves, ST: stem.**



(d) Feeding



(e) Feeding



(f) Availability

**Figure 5- 3 (B) Seasonal changes in the use of food items. In the feeding charts, percentage on Axis Y was calculated using data of feeding records of a given food item divided by the total feeding records multiplied by 100%. In the availability chart, percentage on Axis Y was calculated using the actual scores divided by maximum potential scores. FLBD: flower buds, OPFL: open flowers, IMFR: immature fruits, MFR: mature fruits.**

peaked in May. Feeding on mature fruits peaked in November 1997, but their availability peaked in October, a month before the feeding peak. This indicates that feeding on flowers and fruits was not influenced by their availability. Further, flowers and fruits were available all year, but feeding on them reached only in the lean season between November 1997 and February 1998 when the availability of young leaves reached the lowest level in, and also did feeding on young leaves. Thus it is suggested that young leaves were the preferred foods of white-headed langurs. Flowers and fruits were keystone plant resources that were only used in the lean season. This is different from other primates. For example, the folivorous diet of mountain gorillas (*G. gorilla*) seems to be the outcome of degraded habitat constraints; *i.e.,* if fruits are available, mountain gorillas would eat more fruits and their diet would be more frugivorous (Rogers *et al.*, 1992). According to Dasilva (1992), black-and-white colobus monkeys (*C. polykomos*) switched their diet from seeds (preferred food item) leaves when seeds are not available.

*Cuscuta chinensis* is a parasitic climbing plant without leaves. Its stem is succulent and rich with water. The peak of feeding on this item fell well in the dry season (around December 1997). This seemed to be related to water requirements and will be discussed below.

#### *5.3.1.7 Seed predator or disperser?*

There were 65 records of feeding on fruits and seeds, including 12 species from 7 families (*Table 5- 10*). Langurs ate seeds of *Caesalpinia sappan, Millettia pachycarpa*, and *Sterculia euosma* and discarded fruit pulp. In faecal samples, there were no complete seeds found between November 1997 and September 1998, indicating that white-headed langurs digested seeds along with fruit pulp. Thus, as is the case in other leaf monkey species, the white-headed langur was a seed predator, not a seed disperser.

#### *5.3.1.8 Mineral intake or insectivorous behaviour?*

There were 20 systematic records of licking a rock surface (Chapter IV), in addition to 15 opportunistic notes. Licking behaviour was a common activity in white-headed langurs in the reserve, which sometimes lasted for up to 1.5 hr. Langurs carried out this activity in cavities. These cavities were also the places where a kind of grey powder was formed on the rock surface (*pers. obs.*). However, small insects (*e.g.*, ants) were found on the rock surface everywhere. So it was not certain what was licked by langurs due to the distance of observation. Both insects and minerals may be taken (Struhsaker, 1975; Struhsaker *et al.*, 1997; Oates, 1978, 1994; Kay & Davies, 1994), but it seemed more likely that langurs were licking the grey powder, because the licking behaviour was found only in these cavities and not at other places where insects also occurred.

#### *5.3.1.9 Water drinking*

Water accumulated in seasonal ponds during the rainy season in 1997 and was available till April 1998 (Chapter II). There were 3 systematic records of langurs drinking water from the seasonal ponds (see *Table 4- 5*) and 6 opportunistic records. All these records were obtained in the winter (from November 1997 to January 1998). The period fell in the dry season (see *Figure 2- 6*) when langurs fed on more mature leaves. The behaviour was not seen in other seasons in any langur groups. Two instances of drinking water were witnessed by C.M. Huang (*pers. comm.*) in the winter of 1996. A possible explanation was that water in the food was not enough to meet the metabolic requirements in the dry season (*i.e.*, the winter), and langurs had to drink water from the ponds. Thus the seasonal water bodies may be an important resource. This explanation was supported by the langurs feeding on the succulent stem of *Cuscuta chinensis* that was rich with water. Its feeding peak fell in the same season.

### 5.3.2 Habitat use

#### *5.3.2.1 Range use*

*Figure 5- 4* shows the distribution of range use by the 13 study groups. It is shown that all-male bands, GA1 and GA4-B, had large ranges. Their ranges were not

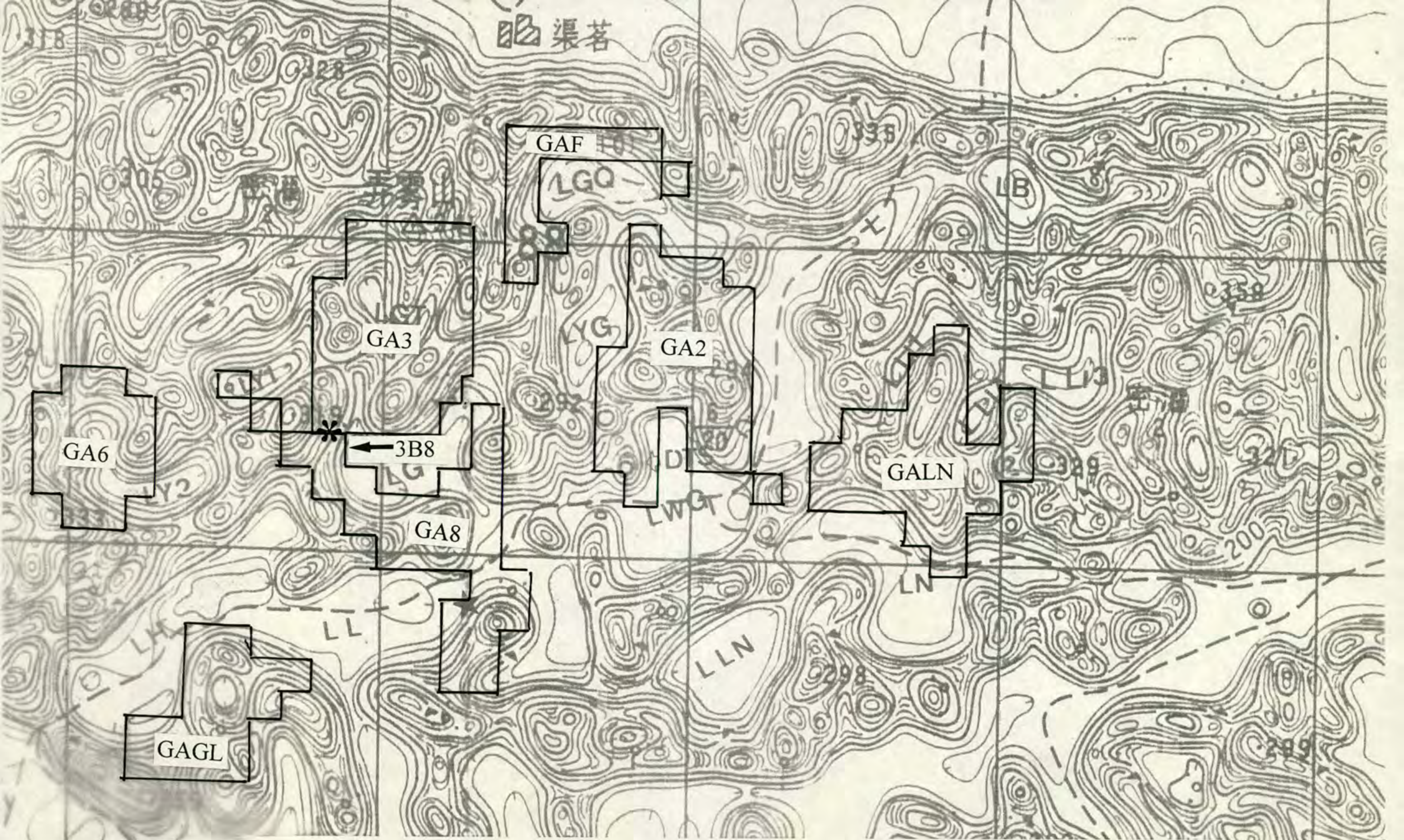


Figure 5- 4 Home range distribution of the study groups of the white-headed langur.

( ★: the campsite)   Scale: 1 : 15.873

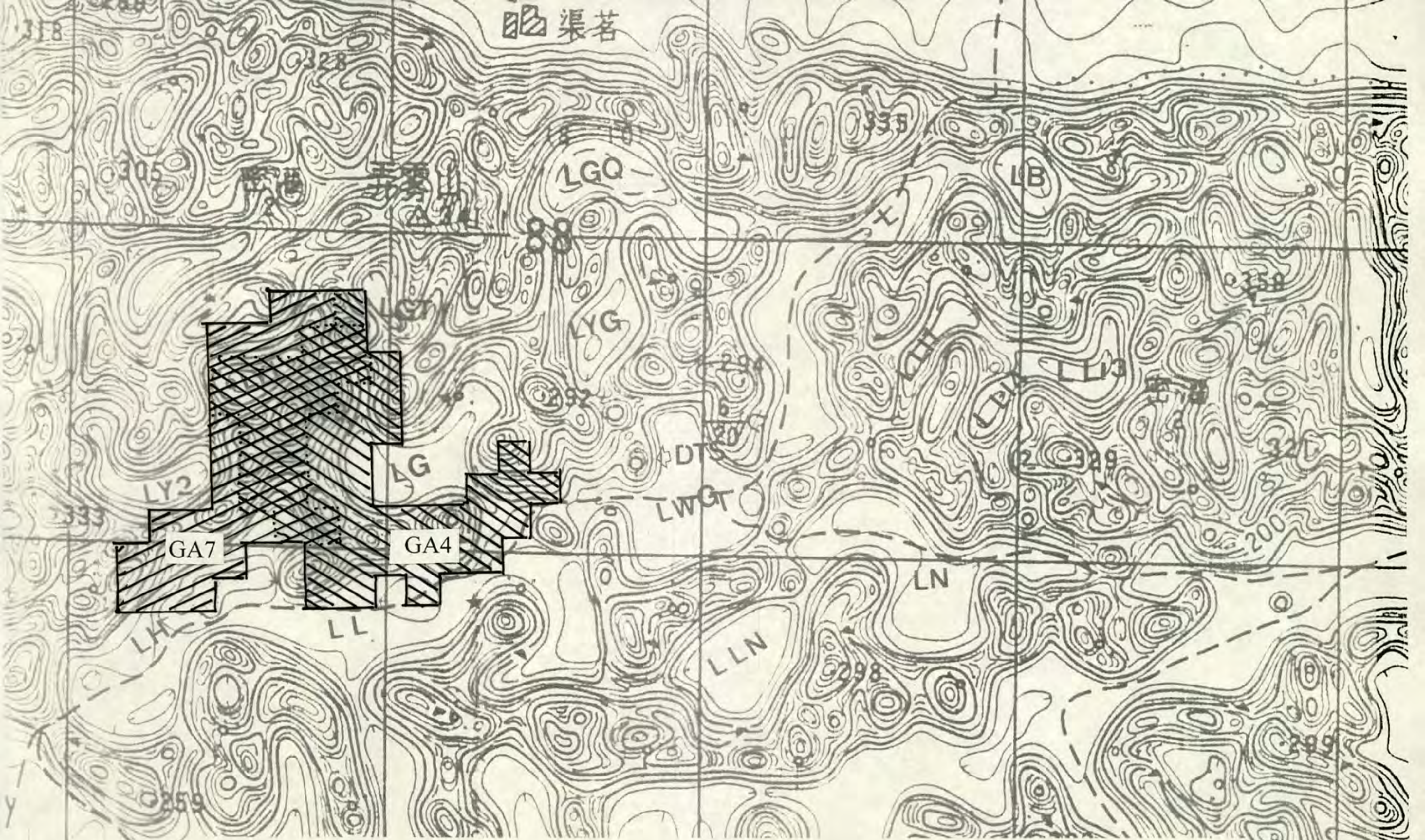


Figure 5- 4 Home range distribution of the study groups of the white-headed langur.

( ★: the campsite) Scale: 1 : 15,873

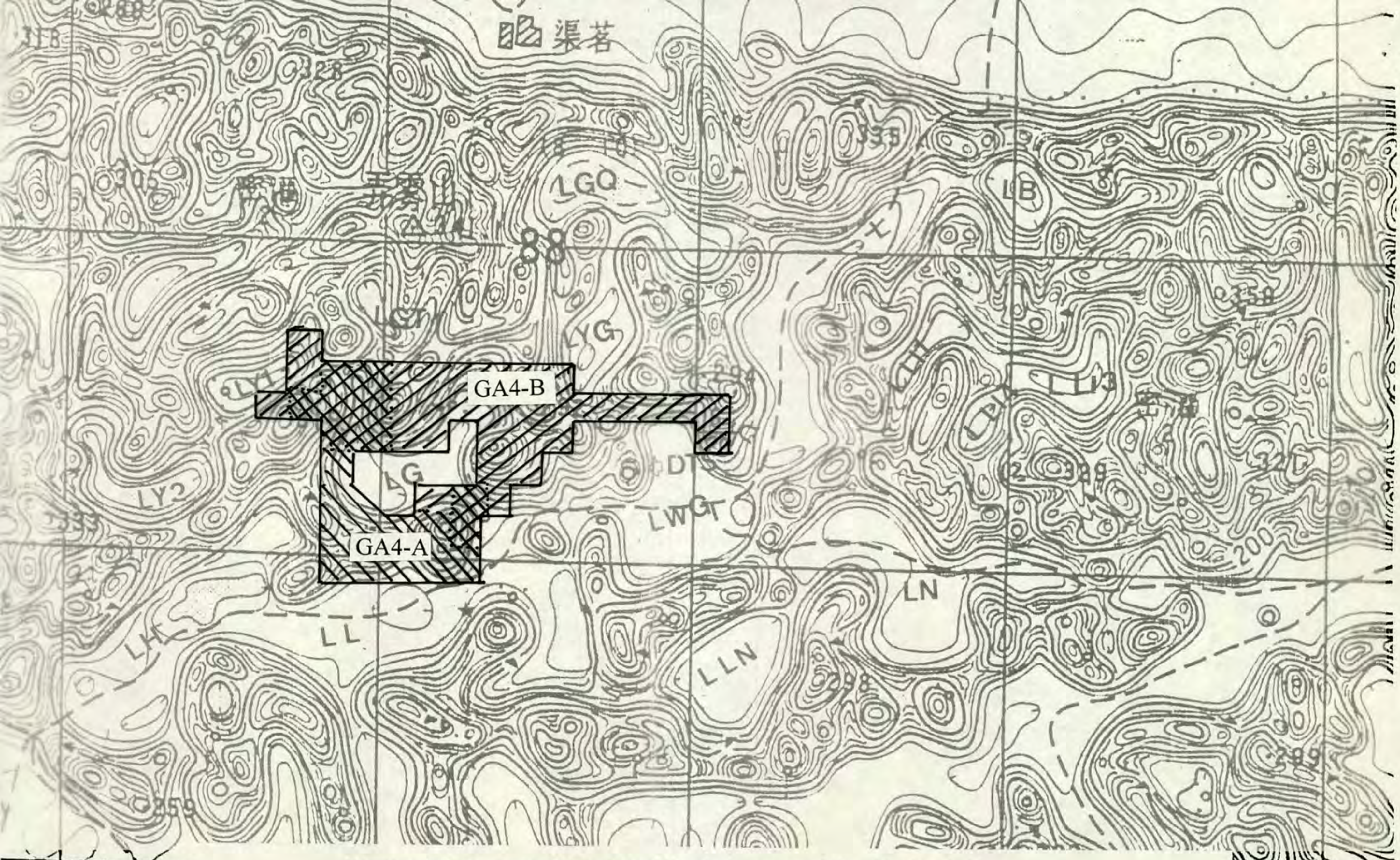


Figure 5- 4 Home range distribution of the study groups of the white-headed langur.

( ★: the campsite) Scale: 1 : 15,873

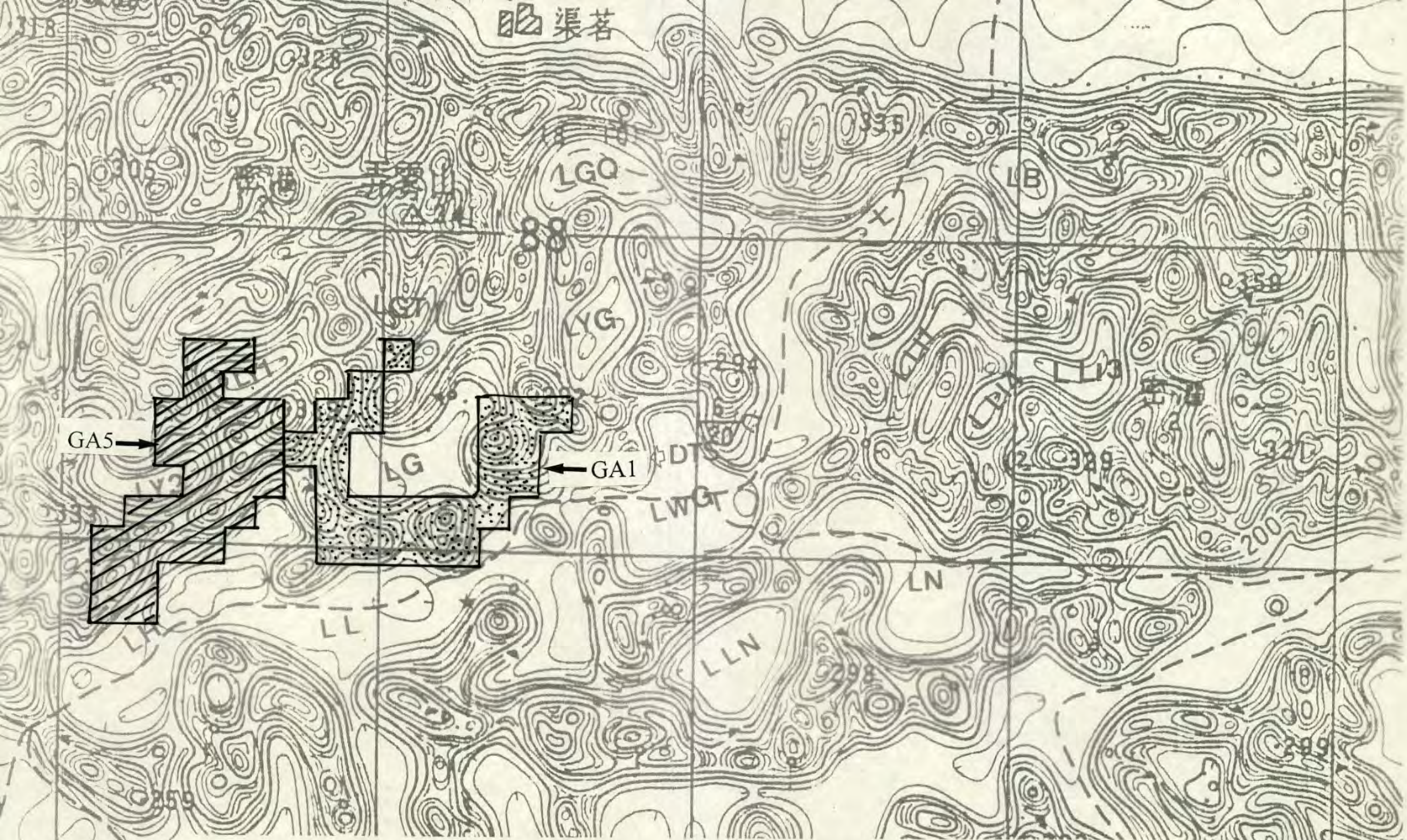


Figure 5- 4 Home range distribution of the study groups of the white-headed langur.

( ★: the campsite) Scale: 1 : 15,873

defended. Larger bisexual groups (*e.g.*, GA3 and GALN) had a well-defended and smaller range. Compared to larger groups, smaller bisexual groups (*e.g.*, GA8 versus GA3) had a larger and poorly defended range. The valley LG was a place where several groups (*i.e.*, GA1, GA3, GA8, all male bands, and some unidentified individuals) often met. GA8 shared its range with all-male bands (GA4-B and GA1) if the inter-group distance was ≥ 150m. When these bands stayed in GA3's range, they were chased away by the breeding male of GA3. Range use by different groups often overlapped spatially, but not temporally.

It is shown in *Figure 5- 5* that when 86 records of the location of GA8 were obtained, its full size of home range could be defined, because the home range size did not increase further. So it was assumed that the home range size of GA8 during the observational period (shown in *Figure 5- 4*) had been completely delimited. Using this point of levelling off to evaluate the home ranges of other langur groups, it was seen that the part of the home range of GA3 and GA4 that was in the main study area could be well defined, and the home range size of GA2 would not have increased significantly with more records (*Table 5- 12*).

The range of GA1 overlapped with that of GA3 and GA8 by about 65%. In contrast, there were no records of range encroachments between groups GA2, GA3, GA8, and GAF. There were observations of inter-group interactions between GA3 and GA8 (detailed in Chapter VI). The interactions took place precisely at the same locality (3B8, *Figure 5- 4*). GA2's range did not overlap with that of GALN, nor did GA6 with GA4 first or with GA7 later. GA7 appeared in the valley LY1 during a male replacement occurring in GA4 from December 1997 to January 1998 (see Chapter VI). Soon after this event, GA5 moved out of its range, which was then used by GA7. Though LY1 was still used by other langurs, the invasion took place only when GA7 was absent. GA3 was found to invade LY1 in only three cases, and GA8 in only one case. The overlap area between GA3 and GA7 accounted for 8.5% of GA7's range and 11.1% of GA3's. That between GA4 and GA3 accounted for 38.1% of GA3's and 25.5% of GA4's. The overlap between GA4 and GA5 accounted for 27.6% of GA4's and 40.6% of GA5's range. It is worth emphasising that the overlap of GA4 with other groups was considerable. This may be an unusual situation,

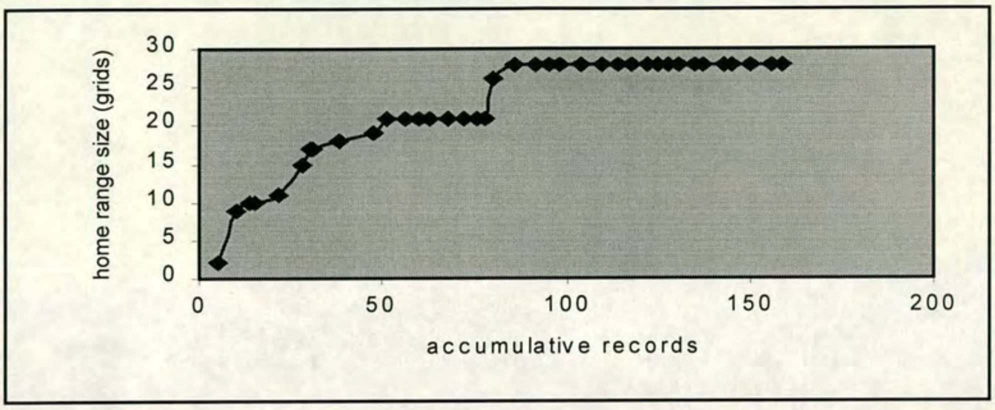


**Figure 5- 5 Relationship between home range size and observational records of white-headed langurs (data from langur group GA8).**

Table 5-12 Hourly range and overall range use by bisexual langur groups

| Groups | Records | Ranging[1] (m) | Mean GS[2] | No. Inf.+Juv. | Habitat[3] Quality Index | Range Size (ha) | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | Observed | Predicted | difference |
| GA2 | 82 | 40±14 | 6 | 0 | 2 | 32 | 18.6 | 13.4 |
| GA3 | 218 | 52±8 | 14.5 | 7 | 4 | 31.5 | 24.8 | 6.7 |
| GA4 | 145 | 69±15 | 10 | 2 | 3 | 48 | 20.7 | 27.3 |
| GA5 | 54 | 166±100 | 7.5 | 2 | 3 | 26 | 16.5 | 15.5 |
| GA6 | 11 | 142±34 | 11.5 | 6 | 4 | 16 | 21.7 | -5.7 |
| GA7 | 55 | 50±15 | 9.5 | 3 | 3 | 36 | 26.9 | 9.1 |
| GA8[4] | 164 | 32±7 | 4.5 | 0 | 1 | 28 | 28 | 0 |
| GALN | 12 | 38±20 | 12 | 7 | 4 | 27 | 18.6 | 8.4 |
| GAGL | 7 | 67±67 | 4 | 0 | 1 | 17 | 24.8 | -7.8 |

1) Ranging indicates the hourly travel speed (see text). 2) Mean group size was used to estimate the predicted home range size. 3) Habitat was scored according to human disturbance on the vegetation (see Chapter 2). 4) Data from GA8 were used to estimate the constant in Furuichi's formula, so they were excluded from the statistical analysis.

because the group was in an unstable social state (*i.e.*, during a group take-over).

A patch of land (some 1ha) was cleared by local peasants on a slope in the valley LWG in January 1998. This slope was on the route used by GA2 to the hill DTS (*Figure 5- 4*). After the disturbance, GA2 did not use this hill for up to 7 months until there was a new immigrant male after the group takeover in late July.

Using the data from GA8, the constant in Furuichi's formula, $\alpha$, was calculated to be 6.2. Predicted range size was then calculated for other groups. *Table 5- 12* shows the results. In the calculations, the max group size was used (see Chapter IV), because at least this number of individuals could be supported by the group's home range. The observed range sizes of only two groups (GA6 and GAGL) were smaller than the predicted sizes. GA6's range in the main study area (LY3) was only a part of their home range; whereas only three observations were made of GAGL, so only a small part of their range was recorded. In all other groups, the observed home range size was larger than predicted, and the overall difference between the observed and predicted range size was statistically significant (Goodness of fit test, $\chi^2 = 74.57$, $df = 7$, $p < 0.01$,).

A primate group often uses part of its home range intensively with only occasional, usually seasonal, forays into other parts (Fleagle, 1988), which results in sampling error in estimating the range area; *i.e.*, range size increases with the number of observations (or records in this instance). However, the Pearson correlation test did not show a significant correlation between the number of records and the range size in the present study ($R = 0.525$, $n = 9$, two-tailed, $p = 0.147$). This indicated that the estimate of the area of range use by the 9 langur groups was not significantly influenced by the number of observations beyond a certain point, though further observation on some groups might increase the size of area to some extent (also see *Figure 5- 5*). Thus the above difference between observed and predicted home range size may indicate the capacity of the environment to support additional langurs.

Differences in habitat quality influence ranging patterns (see Introduction to this chapter) and activity patterns (Chapter IV). According to the extent of vegetation disturbance, the habitat quality in the main study area was classified into 4 classes on an ascending scale of quality from 1 to 4 (see Chapter II and *Table 5- 12*). White-headed langurs preferred large areas of continuous habitat, not small fragmented areas (Chapter III). In range defence (detailed in Chapter VI), male langurs played a major role. Thus a male's "resource holding power" (Krebs & Davies, 1997) should give a positive correlation between the quality of habitat he occupies and the number of females he monopolises and offspring he sires. Observational data from these langur groups *Table 5- 12* showed a strong correlation between the habitat quality and the group size (Spearman Rank correlation coefficient $r_S = 0.8875$, $n = 9$, one-tailed, $p < 0.005$). A further test showed a very strong correlation between habitat quality and the number of juveniles and infants in these groups during the observation period ($r_S = 0.9083$, $n = 9$, one-tailed, $p < 0.005$). In the field, young langurs were found in the valleys with the higher three quality indices (2-4), accounting for 50.1% of the main study area (*Table 2- 1*). There was no significant correlation between habitat quality and home range size in these same groups (Spearman rank correlation coefficient $r_S = 0.075$, $n = 9$, two-tailed, $p > 0.1$) or between food plant diversity and home range size (Spearman rank correlation coefficient $r_S = 0.333$, $n = 9$, two-tailed, $p > 0.1$). This may be because changes in home range size are made complicated. On the one hand, home range size increases with group size in homogeneous habitat; and on the other hand, home range size and group size decrease with habitat quality in heterogeneous habitat. Thus, changes in home range size in heterogeneous habitat cannot be predicted.

### *5.3.2.2 Vertical habitat use*

There were 18898 records collected from 12 langur groups, of which only a subset of 10,494 was used, because these records were of clearly visible individuals. GAF was excluded from the analysis due to the presence of a François' langur in the group. Calculations of time spent at different vertical levels were based on the 10,494 records. *Figure 5- 6* shows the general pattern of langur use of different levels of the limestone hills.

It is shown in this figure that white-headed langurs spent much more time at lower levels (lower and hill-foot) than at higher levels (middle and upward). Among the five vertical levels, the time proportion decreased with the height from middle (M) to the top (T), but the difference between these three levels was not significant; and the time proportion at lower level (L) was significantly more (ANOVA One-way test, F=10.17, DF=4, $P<0.01$). The time proportion at hill-foot was intermediate between L and the other (higher) levels, but closer to L. In the field, when langurs stayed on the top of hills for more than 40min, the observer stopped observations and switched to a different langur group, because they would either move away along the top of hills or stay there for the following several hours out of sight. Thus, the actual time spent on the level T should be much more than that shown in this figure. Because of this, data for T were excluded from further analysis. Due to the similarity between U and M, data for these two levels were pooled together and compared with L and H using ANOVA one-way test, showing that langurs spent significantly more time at L and H than U and M (F=19.07, DF=2, $P<0.01$). This pattern of usage was consistent with the vegetation distribution pattern (see *Figure 2- 7* f); *i.e.*, vegetation was mainly distributed at level L in the hill-group LGS. White-headed langurs carried out most of their maintenance activities at these two lower levels, including 81.3% of feeding and 57.6% of resting records. Data from GA1, GA2, GA3, GA7, and GA8 were analysed using discriminant analysis, which showed that there was no significant difference between the groups in vertical habitat use (ANOVA, $p > 0.05$). It was found in the field that white-headed langurs stayed in trees on the flat ground ($n = 2$, one in the valley LY1, the other in Longgang Reserve) when no humans were present. The langurs ran on the ground to traverse from one hill to another ($n=1$, in the valley LL). This indicates that levels L and H were the favourite habitat of langurs, and other levels of the hill groups may be a refuge for langurs to avoid humans.

Because the lower two levels (L & H) were the major area used by langurs, data from these two levels were pooled together and analysed to test for any seasonal changes in level use. The result showed no seasonal difference in the use of these levels by langurs (Kruskal-Wallis test, $K = 2.21$, $p > 0.05$).

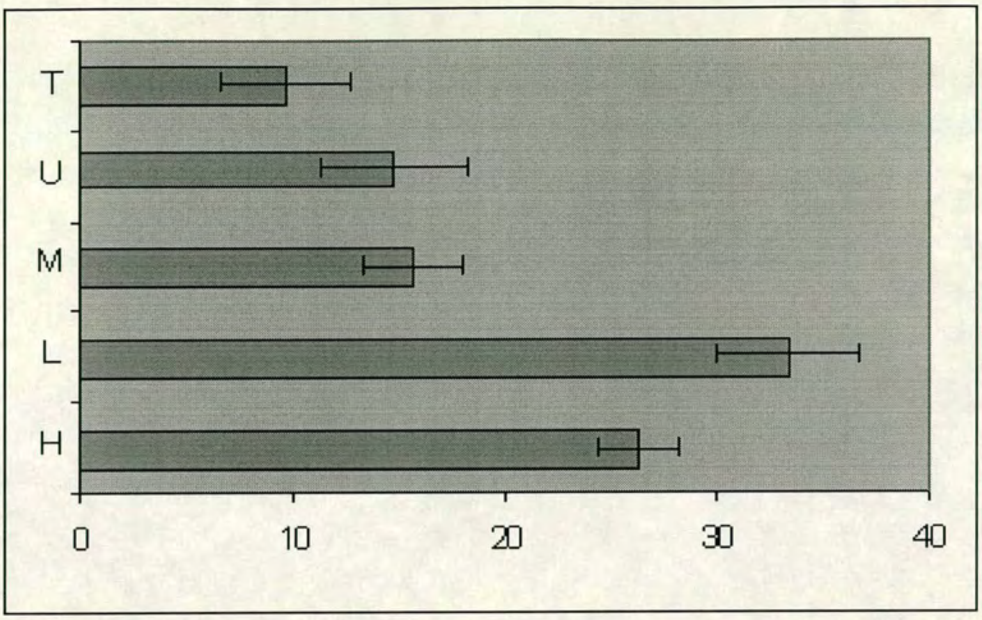


**Figure 5- 6 Vertical habitat use (time proportions spent) by white-headed langurs. Y-axis represents the vertical levels from hill-foot (H) to hill top (T), and X-axis the proportions of observational records ( in %). On each bar, a standard error is shown.**

## 5.4 Discussion

### 5.4.1 Dietary adaptations

Results showed that white-headed langurs fed mostly on a diversity of less common plant species (*Table 5- 1* and *Table 5-* 2). They relied heavily on young leaves (79.1% of feeding records) which showed seasonal variations in availability (*Figure 2- 13*). Only in the lean season between October 1997 and February 1998 when the availability of young leaves decreased nearly to zero, did langurs feed significantly more on mature leaves (*Figure 5- 3*). The Tana River red colobus monkey has been shown to have a similar feeding pattern (Mowry *et al.*, 1996). However, when feeding on mature leaves, they focused on leguminous species that contained significantly more crude protein (also see Davies *et al.*, 1999). In the present study, however, there was only one leguminous species (*Pithecellobium clypearia*, see *Table 5- 1*) which played an important part in the diet only seldom (*Table 5- 8*), though another 4 leguminous species were available in the environment (Appendix A). One of these 4 species (*Albizzia kalkora*) was among the 20 most common species (*Table 2- 6*). It is worth noting that, in the lean season, the white-headed langur also fed more on flower buds, mature fruits, and the stem of *Cuscuta chinensis*. It is suggested that the plant species used in the lean season may contain more crude protein and/or less fibre than other species then available. Also, the flower buds, mature fruits and stem consumed may compensate for the loss of protein intake due to lack of young leaves and may provide energy as well (fruits). This suggestion awaits support from nutritional analysis of food plants.

Life history is closely related to body size, and body size is in turn related to diet; folivores tend to be larger in body size and brain size (Clutton-Brock & Harvey, 1980; Harvey *et al.*, 1987; Fleagle, 1999). Harvey *et al.* (1987) proposed that body size and brain size are two important factors causing differences in life history. In the genus *Presbytis*, *Trachypithecus* spp. eat more leaves than other subgenera (Bennett & Davies, 1994). *Table 5- 13* shows a comparison of body size parameters and extent of folivory among *Presbytis* species. Obvious differences are shown in diet and adult body size between the subgenera *Trachypithecus* and *Presbytis*. Leaves make up less

**Table 5-13 Comparison of body size parameters and extent of folivory among *Presbytis* species***

| | Fadbdw**(kg) | Madbdw(kg) | Adbrw(g) | Relative brain size | % leaf |
|---|---|---|---|---|---|
| **Subgenus *Presbytis*** | | | | | |
| *comata* | 6.2 | 6.3 | 80.3 | 12.9 | <40 |
| *melalophos* | 6.6 | 6.7 | 80 | 12.1 | 30 |
| *potenziani* | 6.4 | 6.5 | | | <50 |
| *rubicunda* | 6.3 | 6.3 | 92.7 | 14.7 | 40 |
| **Subgenus *Semnopithecus*** | | | | | |
| *entellus* | 11.4 | 18.4 | 135.2 | 11.9 | 50 |
| **Subgenus *Trachypithecus*** | | | | | |
| *cristatus* | 8.1 | 8.6 | 64 | 7.9 | 55 |
| *geei* | 8.1 | 8.6 | 81.3 | 10.0 | folivore |
| *johnii* | 12 | 14.8 | 84.6 | 7.1 | 60 |
| *leucocephalus* | 8.7 | 9.5 | | | 91.4 |
| *obscurus* | 6.5 | 8.3 | 67.6 | 10.4 | 60 |
| *pileatus* | 9.5 | 11.6 | | | 67 |
| *vetulus* | 7.8 | 8.5 | 64.9 | 8.3 | 80 |

* Data for *leucocephalus* come from Li & Ma (1980) and this study; those for all other species are cited from Harvey *et al.*(1987), Stanford (1991), van Schaik et al. (1992), and Bennet & Davies (1994). Data for *comata* and *cristatus* are not available, thus data for their subspecies *thomasi* and *auratus* are cited instead. ** fadbdw: female adult body weight; madbdw: male adult body weight; adbrw: adult brain weight; % leaf: percentage of leaf in diet. Relative brain size (g of brain weight / kg of body weight) is calculated using Adbrw divided by Fadbdw.

than 50% of the diet of the subgenus *Presbytis*, more than 50% in *Trachypithecus*, and the amount of leaf in the diet of *Semnopithecus* is intermediate. Corresponding with this difference is the fact that *Trachypithecus* spp. are larger in body size than *Presbytis* spp., which follows the general pattern among primate species. Data in the table show a significant association between female adult body size and the percentage of leaves in the diet (Spearman Rank Correlation Coefficient $r_S = 0.5704$, $n = 11$, one-tailed, $p < 0.05$), but do not show a significant correlation between adult brain weight and the quantity of leaves eaten. However, brain size is closely related to maternal body size, because the brain is an energetically expensive organ to produce (Martin, 1981b). Thus there was a significant correlation between relative brain size (*i.e.*, the ratio of brain weight/female adult body weight) and the quantity of leaves in the diet (Spearman Rank Correlation Coefficient $r_S = -0.75$, $n = 8$, Two-tailed, $p < 0.05$). According to Jones *et al.* (1995, p219), *Trachypithecus* and *Semnopithecus* shared a common ancestry at about 1.4 MYBP and they shared an older ancestry with *Presbytis* (about 1.8 MYBP). It seems that *Presbytis* evolved to be smaller in body size and more frugivorous, whereas *Trachypithecus* and *Semnopithecus* evolved to be larger in body size and more folivorous. In its later evolution, colder weather at night (Bennett & Davies, 1994) on the high mountains might have encouraged *Semnopithecus* to be still larger in body size, even though they have evolved to be more frugivorous than *Trachypithecus*. During the same time, the relative brain size of *Semnopithecus* (11.9g of brain weight / kg of body weight) remained smaller than the more frugivorous *Presbytis* (12.1 – 14.7) and larger than the more folivorous *Trachypithecus* (7.1 – 10.4, see *Table 5-13*).

Seed-eating has been regarded as an adaptation to food plants growing on poor soil (Janzen, 1974; McKey *et al.*, 1981; Davies, 1991; Davies & Baillie, 1988; Dasilva, 1992; Gautier-Hion *et al.*, 1993). Plants on such soils will develop toxic secondary compounds or digestion inhibitors against folivores eating their leaves, because the cost of leaf replacement could be too great. In white-headed langurs, seeds did not make up a major part of the annual diet and were eaten only opportunistically. Does this fact indicate better soil conditions in Bapen Reserve than in Cameroon (McKey, 1978; McKey *et al.*, 1981) or Borneo (Davies & Baillie, 1988; Davies, 1991)? To answer this question, more data need to be collected on soil chemistry from Bapen.

White-headed langurs are found only on limestone hills. This distribution pattern may be the outcome of hunting by humans; *i.e.*, these hills function as a refuge for langurs, because they preferred lower levels and the bottom of hills if vegetation was available and humans were not present. It is also possible that they have special adaptations to the limestone habitat; *i.e.*, they need some special minerals, such as calcium, magnesium, or manganese. According to other studies (*e.g.*, O. Oftedal, *pers. comm.*), the plant species assemblages on limestone-based soils are different from those on other soils (*e.g.*, volcanic or granitic). This means that further data should be collected on the nutrient contents of langur foods from laboratory work.

### 5.4.2 Habitat quality and range use

The relationship between home range size and group size can be assessed using a variation of Furuichi's equation: $R = (\alpha N)/Q$ (see above). The variation predicts that home range size increases with group size given constant habitat quality (*i.e.*, in homogeneous habitat), or decreases with habitat quality (*i.e.*, in heterogeneous habitat) given constant group size. When langur groups living in similar habitat (*e.g.*, GA4 and GALN) were compared, home range size tended to increase (from 27 to 31.5ha) with mean group size (from 12 to 14.5 indv./group). When groups living in different habitats (*e.g.*, GA2 and GA3) were compared, similar home range size of GA2 (32ha) in the habitat of lower quality supported a much smaller group size (6 individuals). To maintain the same group size under such conditions, the home range size should be much larger. This is why there was no significant correlation between group size and home range size of white-headed langurs in Bapen Reserve.

The necessity for increased home range size in habitat of lower quality may have decreased the ability of langur groups to defend their ranges. Also, lowered habitat quality may have decreased the defensibility of the home range of langurs because of the increased cost of defense. Increased home range size and lowered habitat quality may be the reasons why larger bisexual groups had a well-defended range but smaller bisexual groups had a poorly defended range. All of these indicate that habitat quality may have played an important role in the socioecology of white-headed langurs.

### 5.4.3 Habitat quality and langur survival

It is shown by comparing *Figure 5- 6* and *Figure 2- 7* (f) that, among the five vertical levels of the hills, white-headed langurs preferred the lower two levels (L & H), carrying out most of their major activities there. Field observation also showed that, when undisturbed by human presence, langurs probably preferred to stay at the hill-foot and in trees on the flat ground. All this appears to indicate that, because the current distribution pattern of vegetation was caused by human activities, the hills may be the only refuge for the langurs from hunting, but not their favourite habitat.

Habitat degradation causes habitat loss in Bapen Reserve. According to the distribution of plant species diversity (Chapter II), it was higher in vegetation less disturbed by humans. The results detailed here show that white-headed langurs tended to eat as many different plant species as possible, and different groups competed for habitat with higher plant species diversity. Furthermore, langurs fed largely on rare plant species. The rarity of these species may be either because they are specialised for rare habitat types or because of their life history/physiology (Hubbell & Foster, 1986). Tree felling may destroy rare habitats. Life history or physiological differences can mean that rare species grow and reproduce more slowly and thus will be unable to recover quickly after felling. In either case, a decrease in the incidence of rare food species would mean that the habitat would no longer be suitable for langur survival or at least for their reproduction. Young individuals (infants and juveniles) spent significantly more time playing, and play is an energy-consumptive activity category (Chapter IV). Thus growth of offspring is costly and cannot be done without suitable habitat. As a result, some groups in poor habitat would not rear young successfully. In this study, young white-headed langurs occurred in only 50% of the study area with suitable habitat; *i.e.*, only about 50% of the main study area was suitable for breeding groups. Thus, in conservation management, unless habitat quality is well analysed, it will be easy to underestimate the space necessary for langur survival.

### 5.5 Summary

1. White-headed langurs fed on 49 identified plant species from 28 families. Some species were eaten seasonally, and others were year-round foods. Of these families, three (Capparidaceae, Moraceae, and Ulmaceae) contributed 53.1% of the diet. Two plant species, *Pteroceltis tatarinowii* and *Ficus microcarpa,* accounted for over 50% of the total feeding records. The food plant species were largely rare species in the community. Food plant species diversity did not change with seasons. There were six keystone plant species that were eaten in the lean season between December 1997 and February 1998, including *Capparis viminea*, *Cuscuta chinensis, Murraya paniculata, Pteroceltis tatarinowii, Sageretia hamosa,* and *Tetraceae asiatica.*
2. White-headed langurs were extreme folivores, with over 90% of feeding records on leaves. Young leaves were the preferred food. When young leaves were not available, the langurs ate more mature leaves so as to survive the lean season. Contributions of flowers and fruits to the diet peaked in the winter between December 1997 and February 1998 (*i.e.*, the lean season). Feeding peaks on flowers and fruits did not correspond to the peaks of their availability, but to the troughs of feeding on young leaves. Flowers and fruits may provide additional nutrients and energy to compensate loss in nutrients in the lean season due to the decreased availability of young leaves and extra expenditure of energy due to the cold weather. This may be used to explain why white-headed langurs did not change their time budgets to respond to the lower temperature in the winter by increasing time resting or feeding.
3. Bisexual groups had a well-defined home range, while all-male bands did not. Langur groups living in poor habitat had a larger home range than in better habitat. Success in occupying a better habitat patch depended on the competency of the male in a group. Through its competency, a male attracted females who

produced offspring. The number of breeding females and the number of offspring were the two important factors affecting group size. Habitat quality was positively correlated with langur group size and the number of offspring in each group.

4. Because of vegetation clearance, white-headed langurs were restricted to the vegetated limestone hills. These hills provided a refuge from hunting. Habitat degradation caused further habitat loss. Of the 532ha of the main study area, only 50.1% was suitable for breeding langurs, and 49.9% only supported non-breeding langurs.
5. Because the langurs competed mostly for less common plant species that needed rare habitat types or sought for habitat with higher plant species diversity, conservation management must involve protecting these plant species as well as their rare habitat types.

Chapter VI

# SOCIAL BEHAVIOUR AND GROUP DYNAMICS

## 6.1 Introduction

### 6.1.1 Social organisation

One of the major differences between Cercopithecines and Colobines is their social structure (Wrangham, 1987; Melnick & Pearl, 1987; Newton & Dunbar, 1994). Societies of colobines are largely polygamous in which a breeding male monopolises several adult females (Newton & Dunbar, 1994), while those of cercopithecines are largely multi-male, composed of several breeding males and females (Melnick & Pearl, 1987). This difference seems superficially to be related to phylogeny, but detailed scrutiny reveals that the social structure is variable even between populations of a species (for summary, see Bennett & Davies, 1994; Newton, 1988b). For example, in *P. entellus*, uni-male groups are more likely to occur in low altitude and multi-male groups in high altitude habitats. The social structure of *P. johnii* differs with forest types, groups living in gallery forest in Mundanthruai containing more than one male (Bennett & Davies, 1994). *Simias concolor* in the north of Siberut lives in polygamous groups and in the south in monogamous groups (Watanabe, 1981) and this difference is attributed to the anthropogenic habitat disturbance in the north (Bennett & Davies, 1994). The best strategy for a male is to join a group of females and try to keep all other males away (Alberts & Altmann, 1995). However, when all males adopt this strategy, male competition for access to the female group will be intense. According to Strier (2000), the outcome of male competition is influenced by females in two respects. Firstly (in behaviour), the size and cohesiveness of a group of females affect whether a single male can maintain exclusive access to the group. In a polygamous group, the resident male must constantly repel any efforts by males from outside to get access to the group females. If there are too many females or these females spread out too far, the male will have difficulty preventing potential male rivals from copulating with these females; in this case, he may tolerate an extra male in the group, thus a multi-male group is formed. Secondly (in physiology), reproductive synchrony of females in a group also influences male competition, because it is difficult for a male to keep track of several oestrous females at once. Through these mechanisms, ecological factors will influence primate social organisation. For example, altitude causes differences in distribution of food resources that in turn causes differences in the group cohesiveness of females. As a consequence, different social systems occur in a population, as shown by *P. entellus* and other primate species (Bennett & Davies, 1994).

This indicates that the major factor influencing a social system may be the trade-off between males and females when it is to the advantage of both to maximise the number of their offspring. However, because of the difference in parental investment, males maximise the number of offspring by mating with as many females as possible and females by seeking for food of high quality (Trivers, 1972). Thus, any factors influencing the ability of males to monopolise females, including the females' behaviour and habitat characteristics (*i.e.*, distribution of food resources), will influence the social system. These factors will be discussed in this chapter.

### 6.1.2 Group defence

Mitani & Rodman (1979) proposed a concept of D-index, the index of defensibility. It is defined as $D = d/(4A/\pi)^{0.5}$, where d = length of the day journey in km and A = area of home range in $km^2$. The defensibility of the range increases with D. When $D \geq 1$, the home range is defensible. A similar analysis by Martin (1981) failed to show any relationship between defensibility and territoriality in primates. In Martin's study, another index, the range traversing index (RTI) was defined as RTI = D (the defensibility index) $\times \pi$. According to this index, territorial populations should be those with the highest RTI value.

Sexual selection theory (Bateman, 1948; Trivers, 1972) suggests that the factors that limit the reproductive success of females and males tend to be different in mammals: access to resources for females, and access to fertile mates for males.

some apparently deceitful behaviour is discussed in the context of territorial behaviour.

### 6.1.4 Infanticide

Infanticide by adult males has been reported from several orders of mammals, such as Rodentia (Svare & Mann, 1981; Huck *et al.*, 1982; vom Saal & Howard, 1982), Carnivora (Packer & Pusey, 1983, 1984), and Primates (Angst & Thommen, 1977; Hrdy, 1979; Leland *et al.*, 1984; Erhart & Overdorff, 1998). In primates, infanticide was first described in Hanuman langurs, *Presbytis entellus,* by Sugiyama (1965). Since then, it has been reported from more than 10 species of Colobinae, Cercopithecinae, Alouattinae, and Ponginae (Struhsaker & Leland, 1987; Boer & Sommer, 1992), but most reports have been obtained from Hanuman langurs. (Hrdy, 1974) proposed a hypothesis to explain this behaviour on the basis of sexual selection. According to this hypothesis, the behaviour benefits infanticidal males, because it shortens females' inter-birth interval (also see Newton & Dunbar, 1994). Some authors do not accept either that the behaviour occurs or the explanation for it (Curtin & Dohinow, 1978; Boggess, 1979, 1984), because they argue that the cases of infant disappearance following group take-over could have resulted from disease, predation, or accidents (Curtin, 1977). It has also been claimed that interbirth intervals were not shortened by infant death and there was insufficient evidence to confirm that infanticidal males did not kill their own offspring (Curtin, 1977; Boggess, 1979). A second hypothesis (the social pathology hypothesis) was therefore proposed, suggesting that infanticide is not an evolved male strategy, but rather an aberrant, incidental result of escalated aggression in populations with high density (Curtin, 1977; Boggess, 1979). It brings no advantage to infanticidal males over non-infanticidal males. The sexual selection hypothesis predicts that infanticide occurs only in polygamous groups, whereas the social pathology hypothesis predicts that it occurs only in high density populations. Based on these two predictions, an analysis of the evidence supported the sexual selection hypothesis (Newton & Dunbar, 1994); that is, infanticide tended to occur in the populations with a high percentage of one-male troops and with lower population density. The third (resource competition) hypothesis was derived from a study of *P. vetulus* (= *senex*) in Sri Lanka, arguing that infanticide will reduce pressure from resource competitors on offspring sired by the infanticidal males (Rudran, 1973).

The first and third hypotheses are not mutually exclusive; instead, both of them can be regarded as sexual selection hypotheses. The first hypothesis invokes competition at reproduction and the third at future survivorship of offspring. In both cases, infanticidal males maximise their long-term breeding sucess by sacrificing the immediate breeding success of females. Infanticide has also been reported from some captive prosimians, which raises difficulties for the sexual selection hypothesis (Erhart & Overdorff, 1998). In strict seasonal breeders such as the Malagasy lemurs, a male would have to wait for several months to breed after the death of an infant, which negates the immediate potential reproductive benefits of infanticide.

According to the sexual selection theory, infanticide will cause reproductive loss to females. Two possible anti-infanticidal strategies have been postulated. One is to form aggressive coalitions of females (possibly relatives) and males (possibly sires) against the infanticidal male (Hrdy, 1977; Struhsaker, 1977; Butynski, 1982). In a polygamous group, females are presumably closely related to one another, thus they will benefit from a coalition. The other is to show post-conception oestrus and mate promiscuity (Hrdy, 1977; Struhsaker & Leland, 1985). These appear to be effective strategies in Hanuman langurs and red colobus to confuse paternity recognition and reduce attacks by infanticidal males on subsequent offspring. For a female whose infant was targeted by an infanticidal male, there is a choice between loss of feeding opportunity while protecting or escaping with her infant and continuing to feed while sacrificing her infant. Hanuman langur females often choose food and accept infanticide by the male, because the immediate cost of losing feeding opportunity is greater than short-term loss in reproduction (Sommer, 1999). This choice will be discussed in this chapter.

## 6.2 Methods

Observations were carried out in the main study area. Langur groups were not habituated, so no detailed observations could be carried out and observation was usually from a considerable distance. All data on group composition, group dynamics, and social behaviour came from daily observations on the 13 langur groups (for details of techniques, see Chapters IV and V). Information on behavioural events was recorded *ad libitum* (Altmann, 1974). During daily collection of scan samples for activity budgets and feeding records, when a behavioural event occurred (*e.g.*, an inter-group interaction or challenge by an all-male band to a bisexual group), the scan sampling was stopped. The researcher started to record what was happening in the study group(s), including group identity, time, and the whole behavioural context. When the event was completed, scan sampling was resumed on a different langur group for the rest of that day. Information collected in these opportunistic records formed the basis of this chapter.

## 6.3 Results

### 6.3.1 Dynamics of langur groups

Study groups were introduced in Chapter IV. *Table 6- 1* shows a summary of group dynamics. It was shown that a normal breeding langur group was composed of an adult male, several adult females, and their offspring (if any). Thus the social organisation was polygamous. An all-male band was composed of young males. There was no fighting in group GA4 before the challenge of the all-male band (see Chapter IV), thus it was assumed that the old male was the father and the other young males in the group were his sons. According to the change from GA4 to GA4-B, it appeared that an all-male band was formed usually by brothers (in GA4) at the initial stage, after which young males from outside joined. Such a band was the main challenge to the breeding male in a bisexual group. A male-dominant group (*e.g.*, GA4-B) may be a transitional stage from a bisexual group to an all-male band. Old breeding males became solitary after losing during group take-over.

*(a) Sexual activity:* including presenting and mounting. Mounts with pelvic thrusts were observed between females in GA2. Because my prime concern here was

**Table 6- 1 Dynamics of the study groups of white-headed langurs**

| Groups | Types | Immigr. | Birth | Death | Disappearance | Sexual Activity | | Takeover | Infanticide |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Present | Copulate | | |
| GA1 | all-male band | 1 male | | | 2 males | | | | |
| GA2 | polygamous | | | | 1 adult male | 3 sys.+ 5 opp. | | 07/98 | |
| GA3 | polygamous | | 3 | | | 1 sys.+ 4 opp. | 2 opp. | | |
| GA4 | polygamous | | | | 1 adult male & 2 juveniles | | | 12/97 - 02/98 | 12/97 - 02/98 |
| GA4-a | multi-male | 1 female | | | 1 female | | | | |
| GA4-b | male-predominant | 3 males | | | 1 female | | | | |
| GA5 | polygamous | | 1 | | All the group | | | | |
| GA6 | polygamous | | 5 | | | | | | |
| GA7 | polygamous | 1 female | 3 | 3 infants* | 2 females | 14 opp. | | | |
| GA8 | polygamous | 1 female | | | | 1 sys.+ 4 opp. | 3 opp. | | |
| GAF | polygamous | | | 1 infant* | | | | assumed | assumed |
| GALN | polygamous | | 4 | | | | | | |

Abb.: sys. = systematic records, obtained during scan sampling; opp. = opportunistic records, obtained during *ad. lib.* sampling (see Methods). * These infants disappeared from their native groups, but their mothers were observed, so they had probably died.

reproduction, records of homosexual activity and of sexual activity obtained in group takeovers and immediately after immigration were excluded. Based on this definition, sexual activity was first seen in GA2 on April 18, 1998, when a female presented to the male, but copulation did not take place. There were 11 records of sexual activity, 3 (presents) of which were collected from GA2, 3 (2 presents and 1 mount) from GA3, and 5 from GA8 (2 presents and 3 mounts). All of these records were obtained in the summer. Details are shown Figure 6-1. It was seen that sexual activity of white-headed langurs reached a peak in July and the breeding season was assumed to extend between June and August.

*(b) Birth:* Data from the 13 identified langur groups showed that there were 16 births in 5 langur groups. Three births occurred in GA3 (one 01-10/12/97, one 26/02-03/03/98, and one 08-30/06/98), one in GA5 (22/01 –17/02), five in GA6 (23/12/97 – 19/05/98), three in GA7 (25/02 – 08/04), and four in GALN (21/11/97–20/04/98). Furthermore, the two infants that were in GA3 at the beginning of observation were between 6 and 12 months old, which indicated that they were born between 01-05/97. The infant in GA5 at the beginning was around 6 months old, which indicated that it was born around 06/97. The infant in GAF was around 6 months old, thus it would have been born around 02/98. The age of infants in GA6 at the beginning of the observation could not be estimated due to the poor observation conditions (*i.e.*, none of the infants was observed for enough time). For the 5 births in GA6, the date of birth was estimated by calculating the middle point of the two dates; *i.e.*, these infants were probably born in early March 1998. In the same way, the three infants in GA7 were born in mid-March 1998 and the four in GALN in early February 1998. These data are plotted in Figure 6-1, which shows that white-headed langurs gave birth in the winter and spring, starting in December and reaching a peak in February. They did not give birth in the autumn. There were 6 months from the peak of sexual activity (July) to the peak of births (February). This presumably indicates a gestation period of 6 months, which is similar to other colobine monkeys (Napier & Napier, 1967; Harvey *et al.*, 1987; Sommer, 1999).

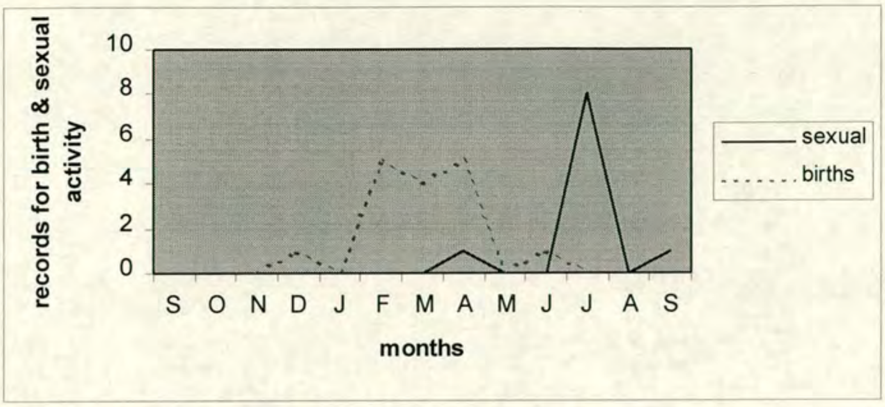


**Figure 6- 1 Temporal distribution of sexual activity and births of white-headed langurs**

*(c) Death:* Data from these 13 langur groups showed that 22 individuals disappeared, including the whole of group GA5 (*Table 6- 1*). Of these 22 individuals, 6 young langurs (the 2 juveniles in GA4, the 3 infants in GA7, and the infant in GAF) may have died from predation or infanticide. Others might have moved out of the study area.

*(d) Poaching:* According to police records, 3 langurs were poached in 1996. One langur (see *Plate 6- 1*) was trapped in the same year, but the event was not recorded in the police files. In each case, a trap was used, so only one langur was removed from the habitat. According to C.M. Huang (*pers. comm.*), there was another poaching event that was not noted in police records. No poaching was recorded in 1998. Local people reported poaching, but accurate numbers were not available. In the main langur population pool (*i.e.*, the hill-group LGS, see *Figure 2- 3* and *Table 3- 3*), poaching of langurs was not detected and langur captures approved by government did not take place during the fieldwork period. Thus, in the main population pool, hunting might not have been the major threat to white-headed langurs, though it was more serious in other hill-groups in Bapen Reserve.

### 6.3.2 Social roles played by group members

White-headed langurs appeared to be living in a peaceful society. It was not easy to see a hierarchical organisation in these langurs, because there was little aggressive

(a) (b)

**Plate 6- 1 The skin of a subadult white-headed langur.**

The subadult langur was captured in November 1997 and died a week later. The group came down to the ground to drink water at a pond, which was spotted by villagers. The villagers rushed to surround the group. Most members rushed out up to a hill and thus escaped, but this subadult was captured and sent to Bapen Reserve Station. The station paid the villagers. (a) The skin mounted on the wall for drying; (b) The tail that had been cut off. Local people used the ash of the hair (after being burned) to stop bleeding of a wound.

behaviour (Chapter IV). An intra-sexual dominance hierarchy was detected in two langur groups, GA7 and GA8. The information on group composition presented in Chapter IV showed that there was immigration by a female once in each of these two groups. The immigration took place in GA7 between August 20 and 29 and in GA8 between March 24 and April 3, 1998. During these time periods, the resident females attacked the immigrant females when the latter tried to feed at the same time. About a week later, the immigrant females started feeding after the residents finished, and no attacks were seen. The displacements over food were not seen in these two groups before the immigration, or in other groups during the whole observation period. Thus the feeding sequence was used as an indication of the higher social rank of resident females.

Male dominance was observed only in GA3. In a typical feeding sequence, the breeding male initiated feeding at the hill-foot while breeding females stayed on the cliff. Once he finished and climbed up to the cliff, the females rushed into the forest and started feeding. The group male always took precedence over the females, and no attacks on females were seen. So this sequence gave an impression that males and females alternated vigilant roles. According to the feeding sequence in females, the possibility of alternating vigilant roles could be excluded, because the feeding sequence did reflect differences in social ranks. Another indication of hierarchical relationships was the priority of access to a small hollow when it rained. At the right-hand hill to LYE, there was only one small hollow at a lower level on the cliff facing towards LG (see *Figure 2- 5*). Group GA3 often used this hollow. Observations (n = 4) showed that only the male stayed in the hollow when it rained. Such male dominance was not detected in other langur groups. It may be expressed in a subtler way that would be revealed by more detailed study.

In all cases of group movement, the breeding male led his group, moving in front of the group. In six cases (2 from GA3 and 4 from GA2), a group was divided into two subgroups. They stayed apart for ≥ 30min, after which the subgroup without the breeding male moved to join the other, and then they moved away together.

It was also the breeding male of a group who provided protection to the group. In all cases that the observers were too close (N = 17in GA3 and N = 2 in

GA6), the breeding male emitted loud calls and rushed out apart from other group members once observers were detected. In the meantime, other group members moved quietly higher up on the hill. After moving out some distance (≥ 100m), the male approached his group and stayed at the back of the group, which was obviously different from normal group movement in which the male was leading the group. This protective role played by breeding males was further clearly indicated in the following observation.

**February 22, 1998, GA8, 0717 hrs:**

The group stayed overnight above the campsite cave. They came down to the hill-foot to feed. At this point, our dog saw them, rushed toward them and barked. The three females moved up rapidly while the male moved down, moving towards and away from the dog (seemed to be frightening the dog). The male kept at a height just out of the reach of a jump by the dog. The encounter lasted until 1048hrs. During the whole event, the observers could approach the langurs much more closely than normal (≤ 25m). The male langur paid close attention to the dog without regarding the observers. At 0847hrs, the male took food from a female's hand, after which the female ran away immediately.

All these observations showed that the breeding male in a langur group was dominant over the females. He made decisions when moving from one site to another, and provided protection to the females when danger appeared.

### 6.3.3 Inter-group Interaction

During an inter-group encounter, the adult males played a key role in range defence. A group responded to the presence of another group to different extents according to inter-group distance. There were 23 records in total, in 12 cases of which the males just stared at the other groups and no further action was taken. There were 4 cases in which the males vocalised while jumping about and shaking trees on the surface of vegetation and the rock. In these cases, the distance between the two groups was between 100 and 200m. In 7 cases, the males rushed toward the other groups, after which the groups of smaller size moved away. The chasing was preceded with vocalising, jumping about, and shaking trees. The distance between groups was about 100m or shorter. There was one case in which a group of small size (n = 4) emerged from the forest in LY1 after group GA3 (n = 15) moved out of the valley. The following was a typical event.

**May 27/98, 0829 hrs**:

A group coded as Un-id. 2 was beside GA8 in LG; they could see each other and were at a distance of ≈ 100m, but no obvious interaction was seen between them. Two males were identified in Un-id. 2. The adult male in GA8 (GA8-male) stared at Un-id. 2. Later, he rushed toward Un-id. 2, the members of which retreated (moving out of the valley) and disappeared afterward. The male came back to his group (GA8) at 0850hrs. Before coming back, he emitted a loud call at the locality 3B8 (see Figure 5-4). At 0856hrs, the adult breeding male in GA3 (GA3-male) approached GA8, emitted loud calls at the same locality, and then stayed there for 9min without further moving. During movement of the GA3-male, GA8 moved away from the locality and kept a distance ≤ 30m from the GA3-male. After staying at locality 3B8, GA3-male emitted loud calls and moved quickly back to his group. This time, the GA8-male did not respond at all, but stayed in bush. The latter interaction between GA3 and GA8 lasted about 15min. Locality 3B8 was on the border line between the ranges of GA3 and GA8, because all records showed that the two groups always stopped there in all cases without further encroachment (n = 17). Thus the two groups stayed in their own ranges.

In another event at the same locality between GA3 and an unidentified group at 1822hrs on Sept. 6, 1998, the unidentified group was driven out of the valley completely, after which the GA3-male retreated back for 20m and kept vigilant for 5min. Before the interaction, the unidentified group fed on leaves in GA3's home range for about 20min, during which they made loud noises; meanwhile, GA3 was moving gradually toward LGT. An individual in the unidentified group emitted loud calls on the hilltop. At about 1842hrs, the GA3-male suddenly emerged from the forest near the invading group and rushed toward them. During the whole encounter, the GA3-male emitted calls of low pitch, which was different from the event described above. GA3 did not use loud calls during this interaction.

In one case there was no obvious response observed though the distance between groups was only about 50m. The event took place between an all-male band and GA2 between 1731 and 1835hrs on September 8, 1998. The adult male in GA2 tolerated the presence of the all-male band at a short distance. The GA2-male came from this band which challenged the original GA2 in a group take-over earlier (detailed below).

In these 23 records of inter-group encounters, there was no case where females were involved in the interaction.

### 6.3.4 Group take-over

**GA4:**

Group take-over took place three times during the observation period. The first event occurred in GA4 in the winter of 1997. The first sign of the group take-over was detected on November 17, 1997, when an all-male band was approaching, which caused agitation in the group. Between December 1 and 6, frequent fights occurred. From December 4, at least two males were found to stay with the GA4 group members. On December 5, a male was rushing about and bit a juvenile in the process. On December 10, an adult female presented three times toward an adult male during a 2.5h observation, and copulated with the male once. The copulation lasted for 15s. Before the beginning of December, copulation was not observed in this group. My earlier study (Li & Deng, 1993) suggested that a female Tibetan macaque (*Macaca thibetana*) used copulation to deal with the presence of a new $\alpha$ male and copulation was used as a tool to compete for social rank. So it was assumed that the resident breeding male had been driven out of GA4 on December 10. Another two copulation events were seen on December 23. The female initiated the event by presenting. GA4 did not break up immediately, but two subgroups were obvious, one (GA4-A) including 2 adult males and 3 adult females, the other (GA4-B) including 5 adult males, 1 young adult female, and 1 subadult male. The two juveniles were no longer seen. Fighting was observed between these two subgroups in January 1998. They stayed together until late February, but the distance between them increased; and from February 25, these two subgroups were no longer seen together. Both of them lost the original home range of which the core area was located in LY1 and was taken over by GA7. GA4-A disappeared from the study area in early April. The female in GA4-B disappeared in May. In the same month, 2 males joined GA4-B. On May 26, more males joined GA4-B and its band size increased to 13. On June 3, the band size returned to 8. From then on, the band size fluctuated between 8 and 10 langurs. Members moved in and out frequently till the end of the observation period.

**GA2:**

The breeding male of GA2 was replaced by a male from GA4-B. The first challenge was detected on June 3, 1998, by GA4-B keeping contact with GA2; but no fighting was observed until July. A serious fight occurred on July 23. At 0836hrs, a copulation took place, after which the female presented again to the new male (a GA4-B member) and was attacked by the group's breeding male. The female rushed away from the breeding male. At 0849hrs, the female presented twice again and the new male moved to stay with her. At 1001hrs, a different female presented to a different male, which was followed by a copulation event at 1004hrs. During this time, the resident male was busy herding his females away from the challengers and fighting with them. At 1025hrs, the resident male and 4 females were far away from the challengers, and one GA2 female stayed with the challengers who were following behind GA2. Four days later, GA2 was found to be headed by a new male who was larger in body size and darker in fur colour than the original resident male. The whole takeover took around 2 months. Compared to the takeover in GA4, this was a shorter time period, group size remained stable, and female membership of the group did not change. Only the breeding male was replaced.

**GAF:**

On August 20, 1998, a male-band challenged this group, during which the infant was heard to scream in the forest. Fights occurred between the resident male and outsiders. On August 26, the infant was found to have disappeared from the group. Because this group was observed for only a short time, the duration of challenge could not be estimated.

### 6.3.5 Infanticide

No infants were seen to die from injury by immigrant males during these three group take-overs. Two juveniles in GA4 and an infant in GAF disappeared immediately after serious fights. Although this suggests possible infanticide, their disappearance could have been due to predation by raptors. The crested serpent eagle (*Spilornis cheela*) occurred in the study area (for detail, see Qian, 1995). According to field observation, white-headed langurs were agitated when these raptors flew over them.

This eagle was 59-64cm in body length and big enough to catch an infant white-headed langur. A nest was found at the west end of LGQ (see *Figure 2- 5*), which was in GAF's home range and was about 100m from the core area in LLGQ. However, the juveniles that disappeared from GA4 were probably too large for capture by a serpent eagle. So it is suggested that immigrant males committed infanticide.

### 6.3.6 Deception

White-headed langurs used loud calls to signal to other potential groups nearby. While vocalising, signallers also jumped about and shook trees vigorously. Because jumping would be costly in terms of energy expenditure, the signal may also function to show the signallers' locality and strength. Compared to jumping, vocalisation may be less costly. Vocalisation alone was used by old solitary males, and it is suggested that this was a dishonest signal of group presence. This is indicated in the following observations.

**January 16: 1714hrs**

A solitary male emitted loud calls twice on the cliff and then 4 times in the bush of the hill beside the campsite. It was not clear if there were any other langurs nearby. The most obvious difference between this langur and other vocalising langurs was that this solitary hid in the vegetation, and did not jump about vigorously or shake trees.

Similar events were recorded on two other occasions with the same individual.

**March 13: 0920hrs**

A solitary male was found in the valley LH. He repeatedly emitted loud calls and shook trees in the bush. Sometimes he emerged from the vegetation and was visible, but the site that he emerged from changed. Each time, he did not stay on rock long before going back into the vegetation. He would jump into the vegetation noisily at one site and then reappear silently at the vegetation surface at a different site. This activity continued till 1003hrs when a group would normally have become inactive and stayed in the bush. All of this behaviour gave an impression that a large group was present. This was also the reason that the observer thought it was a group in the initial stage of the observation.

## 6.4 Discussion

### 6.4.1 Social structure and habitat types

Because of the conflict of interest between males and females (Trivers, 1972), social systems should be very variable. Based on the literature, a scheme has been established to illustrate the factors influencing primate social systems (*Figure 6- 2*). For females, food resources are more important than mates (Sommer, 1999), thus the dispersion pattern of females is restricted by the distribution of food resources. When distribution of food resources changes with habitat quality or altitude (causing differences in forest types), changes in the social system may be predicted (Tilson, 1977; Watanabe, 1981). A patchy food distribution pattern caused by a frugivorous diet or high altitude may result in multi-male primate groups when the patch size is large enough (*e.g.*, *Presbytis entellus*, Ripley, 1970; Boggess, 1979, 1980; Grewal, 1984; Newton, 1987; *Simias concolor,* Tilson & Tenaza, 1976) because of the inability of males to monitor dispersed females (Strier, 2000). Due to different life histories, only a few plant species have fruits at a given point of time, thus fruits are sparsely distributed in patches, but leaves are distributed more uniformly. As a result, folivores (*e.g.*, colobine monkeys) are largely polygamous (see *Table 5- 13* for the situation in *Presbytis* spp.), because it is easy for males to monopolise females; in contrast, many frugivores (*e.g.*, cercopithecines) live in multi-male groups (Melnick & Pearl, 1987; Newton & Dunbar, 1994). Exceptions may be found in those folivorous primate species whose females are in oestrus at the same time (Strier, 2000), because one male may be unable to copulate with many females during a short period. Any factor that causes females to adopt a dispersed distribution may result in two alternative outcomes: decreased group size while maintaining the polygamous social system or a change from polygamous to multi-male social systems. It is suggested here that altitude, habitat quality and timing of female sexual activity appear to be three essential factors influencing primate social systems.

The white-headed langur was an extreme leaf-eater (Chapter V). Its food resources were relatively easily available. It had a home range, the size of which was similar to most other *Presbytis* spp. *Figure 6-1* indicates that langurs had a breeding season, but they were not closely synchronised. It has also been found in captivity that white-headed langurs gave birth year round (Lai, *pers. comm.*), indicating that

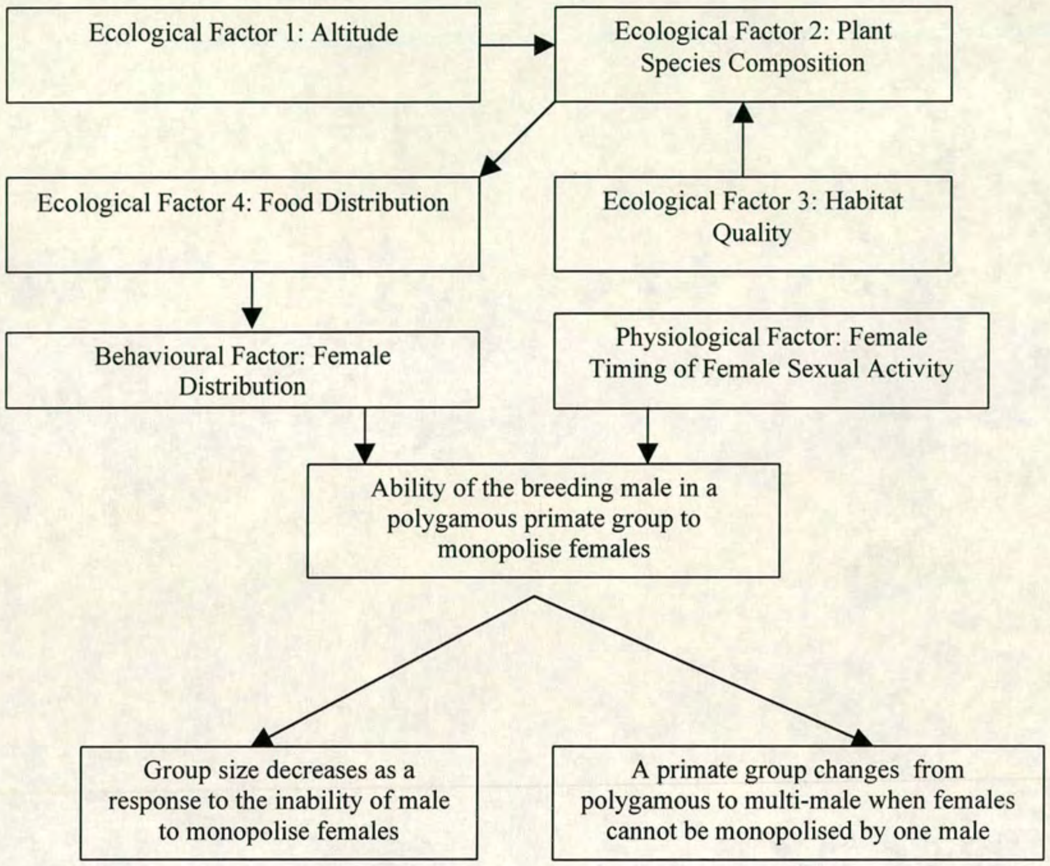


**Figure 6- 2 Socioecological and physiological factors affecting the social system.**

they are not strict seasonal breeders. The range of group sizes of white-headed langurs (4 – 16 animals / group, see Section 4.3.1) fell within the range of other *Presbytis* spp. (Newton & Dunbar, 1994). According to the scheme illustrated in *Figure 6- 2*, all of these factors predict a polygamous social system in white-headed langurs.

### 6.4.2 Competition by white-headed langurs for natural resources

Home range defence has been traditionally regarded as resource defence (see Introduction to this chapter). It can be postulated from sexual selection theory (Bateman, 1948; Trivers, 1972) that the behaviour functions as mate defense for males, or defence of resources that females need. Based on this postulation, two predictions are made for white-headed langurs: one is that the breeding male in a langur group should be active in inter-group interactions, permit females to enter his group, but not permit males to approach his group. The other is that females in the group should be active in opposing any invaders so as to avoid resource competition. Obviously, the interests of males and females seem to be in conflict here, because a male should tend to maximise the number of breeding females in his group, whereas females should tend to reject any genetically unrelated individuals so as to minimise the number of resources competitors in their group.

In the present study, adult males were found to be dominant over females in all situations, including in feeding contexts. This male dominance would override the interests of resident females when attracting immigrant females to the group. New immigrant females had a lower rank (*i.e.*, the situation in the group GA7), indicating that the resident females were reluctant to accept females from outside, though their reluctance did not involve taking part in inter-group interaction. This observation was consistent with the prediction from the theory of resource defence. The breeding males of bisexual groups of the white- headed langur were actively engaged in inter-group interactions and permitted females to join their groups, which meets the prediction of mate defence. Because these female immigrants did stay in their new groups (GA7 & GA8), the group male's interest seemed to have predominated. A resident female could be faced with two options: to repel new female immigrants and risk loss of group membership (and thus of immediate food resources available in the home range) caused by the male; or to be submissive to the male's interest by allowing the immigrants to stay in her group. Suitable habitat quality was vital for females, because otherwise females would not be able to reproduce (see Chapter V). The higher social rank of resident females may minimise any increased feeding competition with immigrant females.

A general pattern of territorial behaviour in the white-headed langur is therefore that the males competed for and defended a home range with habitat quality suitable for reproduction, by which they attracted females.

It is seen here that the dominant male in a group played an important role in the social life of white-headed langurs. Success in competition between groups for suitable habitat quality would depend on the male's resource holding power (RHP, see Krebs & Davies, 1997). According to the vegetation composition analysis (Chapter II), there was a general trend that plant species diversity increased with habitat quality. White-headed langurs preferred a diet of diverse plant species. Thus the group males would compete for a patch of habitat with high food plant diversity. Here, a further prediction can be made: group males with better RHP should possess ranges with higher plant species diversity, attract more adult females, and sire more offspring. There should be a positive correlation between habitat quality and group size (which reflects the number of adult females and offspring) or the number of young. This was the case in white-headed langurs (see Chapter V).

### 6.4.3 Infanticide

Most reports of infanticide have been based on indirect observation (Newton & Dunbar, 1994), as was also the case in this study. Direct observation was almost impossible in the case of white-headed langurs, because the langurs could not be seen all the time and were always observed from a distance. In two (GA4 and GAF) of the three likely cases, young langurs disappeared immediately after serious fighting between resident males and challengers. Death from raptor predation was particularly unlikely in the case of the two juveniles in GA4, because they seemed to be beyond the weakest period. From GA3 in which infants survived well, it could be assumed that pressure from raptors was not great enough to be the main factor causing the death of young langurs. Thus infanticide was more likely the cause of disappearance of young langurs from GA4 and GAF.

It was shown in Chapter IV that infants and juveniles spent a large amount of time playing. White-headed langurs competed for habitat with diverse food plant species and only about 50% of the study area (where the habitat was better) supported reproducing langur groups (Chapter V). All these factors indicated that reproduction may be costly to the habitat. For a female living in a group in this area, to accept infanticide by a new male may mean that she would be able to reproduce again sometime in the future. By resisting or avoiding it, she may have to move out of this area and would no longer be able to reproduce because of the lower quality habitat. Thus the present study supports Sommer (1999) that long-term food supply is more important than the survival of a current infant. Therefore, infanticide may be tolerated in the society of white-headed langurs.

### 6.4.4 Deception

How can the reliability of a signal be guaranteed? Zahavi's hypothesis (see Introduction of this chapter) predicts that reactors always check signallers. This check would involve vision and audition that require appropriate conditions. Such good conditions are not always available especially in forest habitat. In white-headed langurs, the males observed in the present study stayed in the forest and could not be seen moving from a distance. Loud calls could be heard clearly. Jumping involved strength and skill of locomotion. Unskilful locomotion could be lethal to old langurs due to the steep cliffs. Unskilful locomotion would also be detected by potential langur groups nearby. Loud calls combined with tree-shaking in vegetation may function to warn potential rivals of the possible presence of a group. To check these signallers by approaching, signal recipients may risk encountering a strong breeding male who would initiate a serious attack. In such a situation, langurs may have some opportunities for deceptive signalling. Because solitary males did not have a home range (see Chapter V), deception may be practised as an aspect of feeding competition.

## 6.5 Summary

1. White-headed langurs lived in polygamous social groups, containing an adult (breeding) male, several adult females, and their offspring. Young males formed all male bands or male-predominant groups and old males became solitaries after a group takeover.
2. It is suggested that infanticide may be tolerated in the society of white-headed langurs and practiced during group takeovers.
3. Male white-headed langurs defended home ranges in which suitable habitat was available to females. Based on field observations, it is suggested that interests of male reproduction may dominate the society of these langurs.
4. Old males of white-headed langurs may have some opportunities for deceptive signalling. Deception seemed to be practiced as an aspect of feeding competition.

## Chapter VII

# CONCLUSIONS AND RECOMMENDATIONS

### 7.1 Socioecology of White-headed Langurs

Compared to other colobine study sites in Asia, Bapen Reserve, South China, was the driest with the longest dry season and an annual rainfall of about 1168mm during the fieldwork period of the present study (see Chapter II). Due to the flat terrain in East China (*Figure 2-1*), cold air currents caused it to be much colder in Bapen in the winter than in other areas at the same latitude, though Bapen is in the tropical zone. Thus Bapen may not be a benign site. Because of the great seasonal fluctuations in climatic factors, some rare plant species were found in this area. These plant species formed a basis for the feeding ecology of white-headed langurs. Compared to other colobine sites in Asia, Bapen was amongst those with the lowest general diversity of plant species.

The population distribution of white-headed langurs indicated that langurs preferred large continuous habitat fragments. This may be explained by the following fact. In a large continuous habitat fragment, such as LGS, limestone hills were interconnected with each other by high and steep ridges. This prevented intensive human use of the flat ground and natural resources in the valleys closed off by ridges. In these valleys (*e.g.*, LY1 - 3 or LLI 1 - 4), the flat ground was covered with dense vegetation. Local people visited them rarely to collect herbs and other forest products. Rare microhabitat types were thus preserved, which provided living conditions for diverse rare plants on which white-headed langurs fed. Unfortunately, such large continuous habitat fragments have become rare due to heavy human population pressure.

White-headed langurs fed selectively on rare plant species. There were 50 food plant species of which 49 species have been identified (*Table 5-1*). Only eight of them were amongst the 20 commonest species in the habitat (*Table 2-6*). Furthermore, only one of these eight species was highly preferred by langurs. Twelve food species were not encountered in the vegetation analysis (Appendix A). Of the 49 identified food plant species from 28 families, two species, *Pteroceltis tatarinowii* and *Ficus microcarpa*, dominated the diet of langurs, with 50% of total feeding records collected from them, and *P. tatarinowii* was among the 20 commonest species. The other 48 species contributed to the other 50% of feeding records. Plant species are rare either because they rely on rare habitat types that are more likely found in undisturbed habitat or because of their life history/ physiology (Hubbell & Foster, 1986). Thus, rare habitat types may be crucial to the survival of white-headed langurs.

Young leaves contributed most of the diet of white-headed langurs year round, with an annual diet in which young leaves accounted for 79.1% of feeding records; while the availability of young leaves remained below 30% of the maximum phenology score year round. The amount of young leaves in the diet decreased from November 1997 to January 1998 when young leaves were not available due to the lack of rain (*Figure 5-3*). During this period, the amount of mature leaves in the diet increased and peaked, accounting for up to 40% of the feeding records. The amount of other food items, such as flowers and fruits, also increased in the diet, but the contribution was less than 6% of the feeding records. This indicates that the contribution of flowers and fruits was not significant during the lean season, whereas mature leaves were. When feeding on mature leaves, white-headed langurs might be faced with the problem of dealing with fibre fractions that are difficult to digest and secondary compounds that prohibit digestion. White-headed langurs might also obtain less protein from mature leaves. According to Mowry *et al.* (1996), Tana River red colobus monkeys (*Procolobus badius rufomitratus*) concentrate on leguminous species that contain more crude protein and less fibre when switching their diet to mature leaves. A similar tendency is also found in proboscis monkeys (*Nasalis larvatus*) (Yeager *et al.*, 1997). In Bapen, five leguminous species were encountered, but only one species was used by langurs. This species did not play an important role in their diet. It was also found that feeding on flowers and fruits peaked in this lean season, but the peak did not correspond to the peak of their availability, which suggests that flowers and fruits may compensate to some extent energy lost due to the lack of young leaves in langur diet. White-headed langurs had different staple food plant species in different seasons. Seven plant species are regarded as keystone plant species, including *Capparis viminea*, *Cuscuta chinensis, Lindera communis, Murraya paniculata, Pteroceltis tatarinowii, Sageretia hamosa,* and *Tetraceae asiatica.* because they were eaten in large amounts in the lean season. Were the plant species used in the lean season different from other species in chemical components, such as crude protein nitrogen and fibre fractions? Why were these species not used in large amounts in other seasons during which they were available? All these questions remain to be answered after more data are collected from laboratory analysis of food plants.

Compared to other colobine monkeys, white-headed langurs were extreme folivores, with 91.4% of feeding records of leaves (including young and mature). According to Harvey *et al*. (1987), body size is related to the amount of leaves in the diet. However, female body size (measured using body weight) of white-headed langurs was not the largest among the species compared in Table 5-13. According to studies on colobine monkeys in Africa (*Colobus satanas, C. angolensis*, and *C. badius*), populations living in forest on poor soils eat more seeds as a strategy to avoid secondary compounds and fibre fractions that reach high levels in leaves, whereas the populations living in forest on better soils eat more leaves (Maisels *et al.*, 1994; McKey *et al.*, 1981; Gartlan *et al.*, 1980; Janzen, 1974). In the present study, four explanations are suggested for the extremely folivorous diet of white-headed langurs. The first is soil composition; that is, colobine species prefer a large amount of leaves and the extremely folivorous diet of white-headed langurs is supported by good soil conditions in Bapen. However, data on soils are not yet available from Bapen to test this explanation. A second possibility is that there is a wide range of diets in different populations of white-headed langurs, and their diet in Bapen is at one extreme; in other words, a different diet with fewer leaves in it may exist in other populations of white-headed langurs. More data are needed from the field to test this explanation, particularly from the relatively undisturbed Longgang Reserve. Because white-headed langurs appeared to prefer certain fruits when they were available (*e.g., Lindera communis*), the third explanation is that there was less fruit available in Bapen than in other study sites, forcing white-headed langurs to eat a large amount of leaves. To test this explanation, a comparison is needed between Bapen and other study sites, but necessary data are not yet available. The fourth explanation is related to the home range size. Folivorous primates tend to have a smaller home range than frugivorous primates (Oates, 1987). The home range size of white-headed langurs apparently fell in the normal range for colobine monkeys (Chapter V). However, only the hill-foot and lower level of hills provided a large proportion of food resources to langurs, and this area accounted for only a small part of their home range. So, diet quality may be seriously constrained by food supply.

White-headed langurs ate large amounts of the succulent stem of *Cuscuta chinensis*, a parasitic climbing plant without leaves, during the dry season from the end of 1997 to the beginning of 1998 (*Figure 5-3*). Water drinking behaviour of langurs was also observed in this period. It is assumed that white-headed langurs could not obtain enough water from their food, so they visited seasonal water bodies to drink water for metabolism. Thus, these water bodies are vital resources for the survival of white-headed langurs.

Climatic changes (especially temperature) cause differences in energy expenditure of mammals. To deal with extra expenditure of energy so as to keep body temperature stable, langurs would either reduce energy expensive activities or switch their diet to take in foods that contain more nutrients. The current study showed that adult white-headed langurs did not change their activity budgets seasonally (Chapter IV). Food items did not change significantly, although feeding on young leaves did fall to a minimum in 11/97 – 02/98, when the fruits and flowers of *Lindera communis* and other keystone plant species were consumed in large quantities. The only change was in food plant species; white-headed langurs fed on different species in different seasons. Did those species used in the lean season provide more energy or other nutrients to langurs? Further data remain to be collected from laboratory work to answer this question.

Langur groups were largely polygamous, consisting of one breeding male, several breeding females, and their offspring (Chapter VI). After a social change (*e.g.*, male replacement in the group GA4), a normal bisexual group could become an all-male or predominantly-male band (GA4-B), and a multi-male-multi-female group (GA4-A). However, multi-male-multi-female social organisation occurred in very few cases. So the social organisation of white-headed langurs was consistent with that of most other colobine monkeys. Males competed for high habitat quality to attract as many females as possible (Chapter VI). As a consequence, langur groups living in better habitat were larger in group size, and there were more young langurs in these groups. In contrast, there were no young langurs in the groups living in habitat of low quality (Chapter V).

## 7.2 Threats to the Survival of White-headed Langurs

The population size of white-headed langurs has declined by 55.5% over the past ten years, especially since 1991. This decline may be attributed to human disturbance, including habitat fragmentation, poaching, habitat degradation, and pollution by agricultural activities.

Because of edge effects (Lovejoy *et al.*, 1986), rare plant species tend to disappear due to the disappearance of rare microhabitat types after habitat is fragmented. Intensive habitat fragmentation in Bapen Reserve has reduced vast areas of habitat unsuitable for the survival of white-headed langurs (*e.g.*, the hill-group QN, see *Figure 2-3*). Even within a large continuous hill-group (*e.g.*, LGS), fragmentation on a small scale meant that some habitat patches were unused by langurs (*e.g.*, the hill DTS in LWG, see *Figure 5-4*), which further reduced the available habitat area. After disturbance, the flat ground is lost to agricultural use by the local community. It is financially difficult in the short term to purchase all of the land for conservation of wildlife. With an increasing need for land by local people, more valleys will be cultivated by removing rocks or breaching interconnecting ridges using dynamite. Thus habitat fragmentation will continue. When the hill-group LGS, which contains the main population pool of langurs in Bapen Reserve, is intensively fragmented, which is possible in the near future, white-headed langurs will go extinct from this reserve.

According to police records, poaching is another serious conservation threat to langurs outside the main population pool, and has caused the extinction of the langur population in the hill-group GF and a decrease in another hill-group MZ. The future of the langur population in MZ is worrying. White-headed langurs may well go extinct in the foreseeable future if the current situation continues.

Habitat quality of the area (LGS) where most langurs were found in Bapen Reserve was scored according to the extent of human disturbance. This involved the extent of microhabitat loss due to tree felling and vegetation clearance. White-headed langurs fed on rare plant species, which were largely found in higher quality habitat. Thus habitat has been degraded in these valleys that humans often visited, and this has caused white-headed langurs to stop reproducing. Langur groups living in habitat of lower quality (*e.g.*, groups GA2, GA8, GAGL) did not produce offspring (Chapter V). This must be because, in terms of energy, it is costly to rear offspring, and habitat of lower quality could not provide enough rare plant species to sustain reproduction. Only 50% of the main study area in Bapen Reserve supported langur reproduction, although the vegetation of the whole area looked good (Chapters II & V), and, langur groups competed for the central area of LGS with higher habitat quality (more rare plant species). The Reserve Station had argued that tree felling would encourage the growth of young leaves, which would benefit white-headed langurs. This was why they permitted tree felling inside the Reserve. However, they had apparently not considered the effects of loss of rare microhabitat types.

A further problem is that only 5 langur groups were producing offspring in the central area of Bapen Reserve, even though this was the area with the largest population. If the current trend of habitat degradation continues, reproduction may very easily stop completely once the number of rare plant species decreases to some critical value in the near future. Extinction will then become an irreversible trend.

Compared to a monogamous social organisation, polygamy may decrease genetic diversity, because only a few males have a chance to make genetic contributions to the gene pool of the next generation. In this study, adult males competed for high quality habitat to attract as many females as possible, and only 5 males were producing offspring, so only 5 families will be interbreeding in the near future. This may cause very low genetic diversity in this central population pool of white-headed langurs, which could then be faced with problems of stochastic events that cause small populations to go extinct.

As has been shown, seasonal water bodies were important resources for white-headed langurs (Chapter V). These water bodies were polluted by disposal of empty bottles of pesticide (Chapter II). Farmers used large amounts of pesticide on their crops, which could often be smelled from halfway up hills. Pesticide evaporates into the air and may be flushed into soil, after which it may be absorbed into plants and then reach the langurs via their food. This possible threat remains to be investigated with laboratory analysis of soils and langur foods.

## 7.3 Recommendations for Conservation Management

As in other areas of the world, financial constraints have been a major barrier to the improvement of conservation management. Because of this, two alternative actions are recommended: one is *in situ* conservation in Bapen Reserve, the other is *ex situ* conservation by translocation.

### 7.3.1 Recommendations for *in situ* conservation

It is recommended that there should be short, medium, and long term action.

*Short-term action* should aim to prevent langurs from going extinct in Bapen Reserve in the near future. This would involve complete prohibition of poaching in the Reserve and of further habitat degradation in the central area of the hill-group LGS. Keystone plant species must be preserved completely. To prevent langurs from going extinct there, more effort should be made to patrol the hill-group MZ. Furthermore, with some special funding, a few langur groups should be moved from the main population pool (hill-group LGS) to MZ so as to increase genetic diversity of the population in MZ. This may help population recovery in that hill-group. Stopping further habitat degradation in the central area of LGS should guarantee that langurs there will produce offspring. To achieve this, purchase of land in these areas (valleys of habitat types i and ii) should be involved. Land in valleys that are closed off by high, steep ridges is not expensive, which will faciliate its purchase. In fact, purchase had started at the end of this fieldwork, but it is necessary to expand the area involved to include those valleys in the hill-group MZ. During this stage, international conservation organisations might make some experimental small-scale investments, which may not only help to initiate the short-term action in the first place, but also establish the confidence of these organisations in future investment in the area. It will be very new in China that land is purchased for wildlife conservation with financial help from international organisations, which will attract extensive public attention. So this action should be publicised via TV and other media to Chinese Central Government and the general public, which will further safeguard its success.

*Medium-term action* should aim to decrease the need of the local community for natural products (especially firewood) so as to increase the habitat area suitable for langur reproduction. This would involve purchasing the flat ground in the valleys outside the central area (habitat type iii) and prohibiting tree felling in all valleys that have been purchased. To guarantee the success of this action, international conservation organisations, collaborating with Chinese government agencies, should help the local community to switch from trees to other energy sources. This switch may be acceptable, because the local community has been interested in using gas as their daily energy source. During the past several years, more and more local people have used gas (CO) for cooking, but the gas is still too expensive for some families to use. So some way of decreasing the cost must be found. Furthermore, because some land will have been purchased, it will be crucial to maintain the standard of living of local people if further action is to be initiated. A promising solution may be to change their crops from low-value to high-value plantations.

*Long-term action* should aim to remove all agricultural work and tree felling from large areas of continuous langur habitat such as the hill-groups LGS, MZ, GF, and GP (*Figure 2-3*). This would involve purchasing a large amount of land inside these hill-groups, so local farmers would have less land for their subsistence use. Help would needed to increase the productivity (financial output) of their remaining land. Some langur groups could be moved from LGS to GP when the habitat in LGS is filled. All this will need a large financial investment and thus collaboration by the Chinese Government and international conservation organisations will be required. Eventually, the habitat in these hill-groups could be restored, langur population size would increase, and the distribution range of langurs would expand.

It is doubtful whether significant revenue could be obtained from ecotourism in any of the reserves containing white-headed langurs. An ecotourism programme was attempted in Longgang Reserve, but was unsuccessful in attracting visitors. Bapen Reserve is too degraded to provide good wildlife tourism, and has no tourist infrastructure whatsoever.

### 7.3.2 Recommendations for *ex situ* conservation by translocation

If the *in situ* conservation action recommended above is too expensive and is not acceptable financially, the alternative solution is to move white-headed langurs to a new area. A candidate site is Mulun Reserve in Huangjiang County in Northwest Guangxi, around 300km from Bapen Reserve.

Mulun Reserve is 300km² in size, much larger in size than Bapen Reserve (80km², including the distribution range of François' langurs). Most of Mulun is covered with primary limestone forest (*pers. obs.*). The human population is about 9,000, living near and inside the Reserve, the pressure of which (9000/300 = 30 people/km²) is much less than that in Bapen Reserve (18500/80 = 231 people/km²) (Guangxi Provincial Forestry Department, 1993). Highways to this area have not been constructed, thus impacts from the outside world are not great. It is cooler in the summer and colder in the winter, with the lowest temperature of –5 °C in January (Guangxi Provincial Forestry Department, 1993). The mean temperature in July (the hottest month in the year) is 26.9 °C. The Reserve ranges between 500 and 1000m above sea level and receives an annual rainfall of 1500-1600mm. All these features are different from Bapen Reserve but within the range for the habitat of François' langurs. White-headed langurs may be able to survive in this reserve if their basic ecological requirements are not significantly different from those of François' langurs. To initiate translocation, two preliminary tasks should be carried out first. One is to conduct detailed research on the ecology of François' langurs, in an attempt to clarify and compare the basic ecological requirements of white-headed and François' langurs. If their basic ecological requirements are not significantly different, then some langur groups could be moved from Bapen Reserve to Mulun Reserve as a founder population. These groups should be monitored for a few consecutive years, recording their survival status and determining the possibility of moving more groups into this new space.

### 7.3.3 Evaluation of the Recommendations

All these recommendations look too expensive for conserving a single species. However, in addition to white-headed langurs, many other species of plants and animals will also benefit at least from the *in situ* recommendations. White-headed langurs are a flagship species for the area, since they are primates with a beautiful external appearance. It may be more successful to use them to attract public attention, and thus to raise funds for general wildlife conservation in this area. In fact, in both reserves (Bapen and Mulun), there are lots of rare and endangered plant species such as *Amentotaxus argotaenia, Burretiodendron hsienmu, Calocedrus macrolepis, Camellia longangensis, Fokienia hodginsii, Garcinia paucinervis, Keteleeria calcarea, Pinus kwangtungensis*, and *Psoudotsuga brevilolia*. Some other rare animals are also found in these reserves including macaques (*Macaca mulatta*), lynx, ungulates and bears (Guangxi Provincial Forestry Department, 1993; Wang *et al.*, 1989). In Mulun Reserve, there are 30-40 mammal species, more than 100 bird species, 40 – 50 reptile species, about 20 amphibian species, and more than 280 insect species. All these species are valuable natural heritage. Thus the proposed actions deserve attention and financial investment.

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**Appendix A** Vegetation composition of the working area

| Family/Species | Total | LLI1 | LLI4 | LYE | LY3 | LGT | LW | LLI2 | LLI3 | LY1 | LY2 | LYG | LLGQ | LGQ | LB | LGS1 | LGS2 | LGS3 | LGS4 | LWG | LL | LH | LN | LLN | LG |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ALANGIACEAE (527 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Alangium chinense* | 527 | | | | 5 | | 20 | 33 | 32 | 11 | 91 | 9 | 28 | 66 | 60 | | 6 | 14 | 16 | 16 | 44 | 10 | 18 | 20 | 28 |
| ANACARDIACEAE (405 indv., 3 spp., 3 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Pegia bijugu* | 27 | 6 | | | | | 2 | | | | | 5 | | 2 | 5 | | | | 2 | | 3 | | 2 | | |
| 2. *Pistacia weinmannifolia* | 71 | 5 | | 5 | | | 2 | | | | | | | 4 | | | | | | 1 | 44 | 5 | | | 5 |
| 3. *Rhus chinensis* | 307 | | | | | | 2 | 5 | 6 | | 16 | | 7 | 64 | 7 | | | 24 | 6 | 8 | 95 | 14 | 20 | 18 | 15 |
| ANNONACEAE (220 indv., 5 spp., 4 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Dasymaschalon trichophorum* | 1 | | | | | | 1 | | | | | | | | | | | | | | | | | | |
| 2. *Desmos cochinchinensis* | 202 | | | 16 | | | 6 | | 1 | 17 | 9 | 5 | 5 | 14 | 1 | 4 | 15 | 4 | 9 | 25 | 24 | 20 | 1 | | 26 |
| 3. *Fissistigma chloroneurum* | 5 | 5 | | | | | | | | | | | | | | | | | | | | | | | |
| 4. *F. retusum* | 7 | 5 | | | | | | | | | | | | | 2 | | | | | | | | | | |
| 5. *Polyalthia plagioneura* | 5 | | | | | | | | | 5 | | | | | | | | | | | | | | | |
| APOCYNACEAE (16 indv., 4 spp., 3 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Rauvolfia verticillata* | 5 | | | | | | | | | | | | | | | | | | | 5 | | | | | |
| 2. *Strophanthus divericatus* | 2 | | | | | | | | 2 | | | | | | | | | | | | | | | | |
| 3. *Wrightia hainanensis* | 4 | | | | | | | | | | | | | | | | | | 4 | | | | | | |
| 4. *W. pubescens* | 5 | | | | | | | | | 3 | | | | | | | | | | 2 | | | | | |
| ARALIACEAE (71 indv., 3 spp., 3 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Heteropanax fragrans* | 10 | | 6 | | | | | | | | | 4 | | | | | | | | | | | | | |
| 2. *Schefflera arboricola* | 30 | | | | | | | 3 | 4 | | | | | 2 | | 7 | | 2 | 2 | | 6 | 2 | | | 2 |
| 3. *Tetrapanax papyriferus* | 31 | 5 | | 4 | | 2 | | | | | | 20 | | | | | | | | | | | | | |
| ASCLEPIADACEAE (3 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Cryptolepis buchanani* | 3 | | | | | | | | | | | | | | | | | | | 2 | | | 1 | | |
| BIGNONIACEAE (842 indv., 3 spp., 3 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Oroxylun indicum* | 783 | | | | | 1 | 5 | 17 | 18 | 10 | 10 | 15 | 8 | 131 | 18 | 9 | 14 | 5 | 24 | 17 | 40 | 130 | 204 | 97 | 10 |
| 2. *Radermachera si* | 29 | | | | | 2 | | 2 | | 1 | | | | 4 | | | | | | | 9 | 4 | 2 | 4 | 1 |
| 3. *Stereospermum chelonoides* | 30 | | | | | 1 | | | | | | | | | | 1 | 2 | 2 | 3 | 1 | 15 | | 4 | | 1 |
| BOMBACACEAE (64 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Gossampinus malabarica* | 64 | | | | | | 1 | | | 1 | 3 | | | 1 | | | | 1 | 3 | | 2 | 6 | 29 | 16 | 1 |
| BORAGINACEAE (4 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Cordia dichotoma* | 4 | | | | | | | | | | 2 | | | | | | | | | | | 1 | | | 1 |
| CAESALPINIACEAE (209 indv., 10 spp., 3 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Bauhinia brachycarpa var. cavaleriei* | 8 | | | | | | | | | | | | | | | | | | 8 | | | | | | |

**Appendix A** (continued-1)

| | | LLI1 | LLI4 | LYE | LY3 | LGT | LW | LLI2 | LLI3 | LY1 | LY2 | LYG | LLGQ | LGQ | LB | LGS1 | LGS2 | LGS3 | LGS4 | LWG | LL | LH | LN | LLN | LG |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2. *B. championi* | 54 | | 1 | | | | | | 5 | | 2 | 5 | | 2 | 7 | 4 | 5 | | | 11 | 9 | 1 | | | 2 |
| 3. *B. erythropoda* | 2 | | | | | | | | | | | | | | 2 | | | | | | | | | | |
| 4. *Caesalpinia aestivalis* | 49 | | | | | | | | | | | | | | | 2 | 1 | 5 | 3 | 5 | 30 | | 3 | | |
| 5. *C. decapetala* | 33 | | | | | | | | | | | | | | | | | | | | 22 | 3 | | | 8 |
| 6. *C. minax* | 6 | | | | | | | | | | 1 | | | | | | | | | 3 | | | | | 2 |
| 7. *C. nuga* | 5 | | | | | | | | | | | | | | | 5 | | | | | | | | | |
| 8. *C. sappan* | 4 | | | | | | | | | | | | | | | | | | | 4 | | | | | |
| 9. *C. vernalis* | 5 | | | | | | | | | | | | | | | | | | | | 5 | | | | |
| 10. *Zenia insignis* | 38 | | | | | | | | | | | | | | | | | | 2 | 32 | 3 | | | 1 | |
| CAPPARIDACEAE (13 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Capparis viminea* | 13 | 2 | | 4 | | | | | | | | | | | | | | | | 4 | 3 | | | | |
| CAPRIFOLIACEAE (7 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Sambucus racemosa* | 7 | | | | | 7 | | | | | | | | | | | | | | | | | | | |
| CELASTRACEAE (2 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Euonymus laxiflorus* | 2 | | | 2 | | | | | | | | | | | | | | | | | | | | | |
| COMBRETACEAE (9 indv., 2 spp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Combretum alfredii* | 8 | | | | 4 | | | | 4 | | | | | | | | | | | | | | | | |
| 2. *C. incertum* | 1 | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| DILLENIACEAE (6 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Tetraceae asiatica* | 6 | | | | | | | | | | | | 2 | 2 | | | | | | | | | | 2 | |
| EBENACEAE (22 indv., 2 spp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Diospyros dumetorum* | 2 | | | | | | | | | | | | | | | | | | 2 | | | | | | |
| 2. *D. siderophyllus* | 20 | 5 | | | | | | | 3 | | | 5 | | | | | | | | 1 | | 1 | | | 5 |
| EUPHORBIACEAE (2414 indv., 21 spp. + 1 var., 13 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Alchornea rugosa* | 225 | 5 | | | | | | | | 1 | | | 8 | 40 | 8 | 4 | 5 | 6 | 4 | 6 | 87 | 24 | 6 | 5 | 16 |
| 2. *A. trewioides* | 16 | | | | | | | | | | | | | | | | | | | | 16 | | | | |
| 3. *Aporosa chinensis* | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | |
| 4. *Bischofia racemosa* | 102 | | 5 | 6 | 1 | 16 | | 1 | 38 | 7 | 6 | 2 | | | 3 | | | | 1 | 4 | 1 | 5 | 6 | | |
| 5. *Breynia fruticosa* | 3 | | | | | | | | | | | | | | | | | 2 | | | | | 1 | | |
| 6. *B. hyposauropus* | 8 | | | | | | | | | | | | | | | | | 2 | | | | | 6 | | |
| 7. *Bridelia monoica* | 19 | | | | | | | | 3 | | | 2 | | | 1 | | 1 | 4 | | 3 | 2 | | 1 | 2 | |
| 8. *Croton kwangsiensis* | 212 | | | 3 | | | 11 | | 3 | | 8 | 5 | 7 | 7 | 9 | 6 | 7 | 23 | 5 | 15 | 64 | 5 | 18 | 6 | 10 |
| 9. *Drypetes integrifolia* | 9 | | | | | | | | 8 | | | | | | | | | | | 1 | | | | | |

**Appendix A** (continued-2)

| | | LLI1 | LLI4 | LYE | LY3 | LGT | LW | LLI2 | LLI3 | LY1 | LY2 | LYG | LLGQ | LGQ | LB | LGS1 | LGS2 | LGS3 | LGS4 | LWG | LL | LH | LN | LLN | LG |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10. *D. tonkinensis* | 8 | 8 | | | | | | | | | | | | | | | | | | | | | | | |
| 11. *Endospermum chinense* | 5 | | 1 | 3 | | | | | | | | | | | | | | | | | 1 | | | | |
| 12. *Fluggea virosa* | 594 | | 9 | 3 | 15 | 11 | 55 | | 50 | 14 | 32 | 1 | | 80 | 13 | 25 | 16 | 18 | 15 | 55 | 86 | 24 | 30 | 36 | 6 |
| 13. *Glochidion lanceolarum* | 25 | | | | | | | | | 3 | 2 | 4 | 2 | 4 | | | | 4 | 4 | | | | 2 | | |
| 14. *G. philippinense* | 51 | | | | | 1 | | 5 | | | | | | | 2 | 5 | 2 | 3 | 5 | 3 | 23 | | | | 2 |
| 15. *G. puberum* | 2 | | | | | | | | | | | | | | | | | | | | 2 | | | | |
| 16. 1) *Mollotus apelta* | 8 | | | | | | | | | | | | | | | | | | | | 8 | | | | |
| 2) *M. a. var. kwangsiensis* | 404 | | | | 1 | 3 | | | 12 | 14 | 80 | | 5 | 73 | 23 | 13 | | 5 | 10 | 45 | 27 | 9 | 64 | 13 | 7 |
| 17. *M. philippinensis* | 487 | | | 2 | | | 18 | | 17 | 4 | 15 | 13 | 24 | 87 | 17 | 4 | 24 | 29 | 18 | 20 | 90 | 27 | 25 | 33 | 20 |
| 18. *M. repandus* | 36 | | | | | | | | | 2 | | | | | 4 | | | | 3 | | 23 | | 1 | | 3 |
| 19. *Phyllanthus emblica* | 134 | | | | 2 | | 2 | | | | | | 2 | 4 | | 16 | 3 | 1 | | 4 | 34 | 20 | 40 | 6 | |
| 20. *P. reticulata* | 5 | | | | | | | | | | | | | | 3 | | | | 2 | | | | | | |
| 21. *Sapium discolor* | 51 | | | | | | 8 | | 4 | 2 | | 3 | 2 | 3 | 1 | | | 2 | | 1 | 14 | 1 | | 10 | |
| FLACOURTIACEAE (1 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Xylosma congestum* | 1 | | | | | | | | | | | | | 1 | | | | | | | | | | | |
| GNETACEAE (2 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Gnetum montanum* | 2 | | | | | | | | | | | | | | | | | | | | | | | 2 | |
| HAMAMELIDACEAE (75 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Liquidambar fomosana* | 75 | 11 | | | 5 | 7 | 1 | | | 6 | 2 | 21 | | | | | | | | 2 | 9 | 4 | 2 | | 5 |
| HYPERICACEAE (144 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Cratoxylon ligustrinum* | 144 | | | 1 | 3 | | 8 | 2 | 5 | 2 | 11 | 8 | 10 | 15 | 2 | 6 | 7 | 9 | 3 | 7 | 16 | 12 | 5 | 4 | 8 |
| ICACINACEAE (14 indv., 2 spp.+ 1 var., 2 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. 1) *Iodes ovalis* | 7 | | | | | | | | | | | | | 2 | | | | | 3 | 1 | | | 1 | | |
| 2) *I. o. var. vitiginea* | 1 | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| 2. *Mappianthus iodoides* | 6 | | 2 | | | | | | | | | | | | | | | | 2 | 2 | | | | | |
| LAURACEAE (1419 indv., 4 spp., 2 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Lindera communis* | 418 | | 10 | 11 | 76 | 54 | 20 | 5 | | 47 | 40 | 15 | | 41 | | | 3 | | | 18 | 42 | 3 | 5 | 24 | 4 |
| 2. *L. pulcherrima var. attenuata* | 504 | 18 | 435 | | | | | | 51 | | | | | | | | | | | | | | | | |
| 3. *Litsea euosma* | 443 | 4 | | 1 | 3 | | 5 | | 5 | | 5 | | 14 | 76 | 9 | 27 | 14 | 32 | 24 | 41 | 101 | 30 | 25 | 20 | 7 |
| 4. *L. monopetala* | 64 | 7 | | 1 | | | | 7 | 4 | 8 | 1 | 2 | | 30 | | | | | | | 1 | | | 1 | 2 |
| LOGANIACEAE (65 indv., 2 spp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Buddlera lindleyans* | 2 | | | | | | | | | | | | | | | | | | | | | 2 | | | |
| 2. *B. madacascariensis* | 63 | | | | | | | | | 2 | 2 | 2 | | | 21 | 3 | 3 | | 3 | 6 | 10 | | 9 | 2 | |

**Appendix A** (continued-3)

| | | LLI1 | LLI4 | LYE | LY3 | LGT | LW | LLI2 | LLI3 | LY1 | LY2 | LYG | LLGQ | LGQ | LB | LGS1 | LGS2 | LGS3 | LGS4 | LWG | LL | LH | LN | LLN | LG |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MELIACEAE (689 indv., 5 spp., 4 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Chukrasia tabularis* | 1 | | | | | | | | | | | | | | | | | | | 1 | | | | | |
| 2. *Cipadessa cinerascens* | 640 | | 5 | | | | 39 | 12 | 33 | | 56 | 16 | 15 | 75 | 13 | | 25 | 30 | 36 | 38 | 85 | 35 | 63 | 42 | 22 |
| 3. *Melia azedarach* | 4 | | | | | | | | | | | | | | | | | | | 3 | 1 | | | | |
| 4. *Toona sinensis* | 9 | | | | | | | | | | | | | | | | | 9 | | | | | | | |
| 5. *T. sureni var. pubescens* | 35 | | 6 | | | | | | | | | | | | | | | 4 | 4 | | | | 20 | 1 | |
| MENISPERMACEAE (7 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Cocculus laurifolius* | 7 | | | | | 3 | | 4 | | | | | | | | | | | | | | | | | |
| MIMOSACEAE (552 indv., 5 spp., 4 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Adenanthera chinensis* | 9 | | | | | | | | | | | 2 | | | | | | | | | | | 4 | 2 | 1 |
| 2. *A. pavonina* | 12 | | | | | | | | | | | | | 2 | | | | | | | | 1 | 1 | 7 | 1 |
| 3. *Albizzia kalkora* | 477 | 5 | 1 | 3 | 6 | 1 | 14 | | 6 | 4 | 20 | 6 | 8 | 80 | 5 | 14 | 13 | 26 | 21 | 21 | 85 | 48 | 47 | 30 | 13 |
| 4. *Leucaena glauca* | 9 | | | | | | | | | | | | | | | | | | | | 8 | | | | 1 |
| 5. *Pithecellobium clypearia* | 50 | | | | | | 3 | | | | 1 | | | | | | | | | | 38 | 8 | | | |
| MORACEAE (1289 indv., 16 spp., 4 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Broussonetia kazinoki* | 4 | | | | | | | | | | | | | | | | | | | 2 | 2 | | | | |
| 2. *B. papyrifera* | 211 | 4 | | | | | 5 | | 2 | 8 | 14 | 7 | | 41 | 6 | | 5 | 13 | 1 | 10 | 34 | 29 | 3 | 7 | 22 |
| 3. *Cudrania cochinchinensis* | 398 | | | | 10 | | 53 | | 25 | 5 | 13 | 6 | | 95 | 25 | | | 11 | 7 | 27 | 44 | 14 | 35 | 28 | |
| 4. *C. tricuspidata* | 5 | | | | | | | | | | | | | | | | | | | | 5 | | | | |
| 5. *Ficus altissima* | 4 | | | | | | | | | | | 1 | | 1 | | | | | | 2 | | | | | |
| 6. *F. elastica* | 8 | | | 2 | | | | | | | | | | | | | | | | 2 | 3 | | 1 | | |
| 7. *F. gibbosa* | 184 | 7 | | | | | 23 | 2 | 11 | 11 | | | 5 | 18 | 2 | | | 3 | 4 | 18 | 42 | 19 | 10 | 4 | 5 |
| 8. *F. glabberrima* | 72 | | 18 | 11 | | | | | 6 | 7 | | | | 18 | | | | | 12 | | | | | | |
| 9. *F. harmandii* | 46 | | | 6 | | 2 | 2 | | 2 | 4 | 3 | | 1 | 4 | | | | | 1 | 4 | 12 | 4 | 1 | | |
| 10. *F. hispida* | 134 | 12 | | 10 | 4 | 28 | 2 | 9 | 13 | | 4 | | 7 | 5 | 10 | | | | | 4 | 2 | 3 | 8 | 12 | 1 |
| 11. *F. microcarpa* | 12 | | | | | | | | 1 | 5 | 1 | 2 | | | | | | | | 2 | | | | 1 | |
| 12. *F. nervosa* | 5 | | | | 1 | | | | | | | | | 2 | | | | | | 1 | | | | 1 | |
| 13. *F. parvifolia* | 12 | | 1 | | | | 2 | | | | | | | 1 | | | | | | | 5 | 1 | 1 | | 1 |
| 14. *F. subulata* | 5 | | | | | | | | | | | | | | | | | | | | | 5 | | | |
| 15. *F. taiwaniana* | 190 | | 14 | 24 | 3 | 70 | | 12 | | 10 | | 8 | | 22 | | | | 5 | 2 | 10 | | 5 | | | 5 |
| 16. *Meras australis* | 28 | | | | | | | | 20 | | | | | | | | | | 1 | 2 | 3 | | | 2 | |
| MYRSINACEAE (211 indv., 4 spp., 3 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Ardisia depressa* | 199 | | 157 | 2 | | 5 | | | 35 | | | | | | | | | | | | | | | | |

**Appendix A** (continued-4)

| | | LLI1 | LLI4 | LYE | LY3 | LGT | LW | LLI2 | LLI3 | LY1 | LY2 | LYG | LLGQ | LGQ | LB | LGS1 | LGS2 | LGS3 | LGS4 | LWG | LL | LH | LN | LLN | LG |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2. *Embelia ribes* | 1 | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| 3. *Maesa japonica* | 2 | | | | | | | 2 | | | | | | | | | | | | | | | | | |
| 4. *M. montana* | 9 | | | | | | | 2 | | | | | | 2 | | | | | 2 | | 1 | | | | 2 |
| MYRTACEAE (262 indv., 2 spp., 2 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Psidium guajava* | 174 | | | | 2 | | | 2 | | | 20 | | | 2 | | 30 | 53 | 25 | | | 33 | | | 7 | |
| 2. *Syzygium cumini* | 88 | | 2 | | | 2 | 15 | 3 | 5 | | 1 | | | 3 | | | | 1 | 1 | 2 | 24 | 11 | 6 | 6 | 6 |
| OLEACEAE (35 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Ligustrum sinensis* | 35 | | | | 3 | | | | | | | | | | | 3 | | | | 7 | 14 | 3 | | 5 | |
| OPILIACEAE (178 indv., 2 spp., 2 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Cansjera rheedii* | 177 | 23 | 5 | | | | 4 | 5 | 21 | 5 | | 4 | 7 | 17 | | | 5 | 14 | 13 | 11 | 11 | 13 | 9 | 2 | 8 |
| 2. *Lepioncerus latisquamus* | 1 | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| PAPILIONACEAE (261 indv., 10 spp., 5 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Cladrastis platycarpa* | 5 | | | | | 5 | | | | | | | | | | | | | | | | | | | |
| 2. *Dalbergia cavaleriei* | 4 | | | | | | | | | | | | | | | | | | | 4 | | | | | |
| 3. *D. hancei* | 62 | 7 | 1 | 4 | | | | | 5 | | | | | 16 | | 5 | | 5 | 2 | 11 | | | 3 | 3 | |
| 4. *D. hupeana* | 10 | | | | | | 3 | | | | | | | 2 | | | | | | | | | | | 5 |
| 5. *D. pinnata* | 1 | | | | | | | | | | | | | | | | | | 1 | | | | | | |
| 6. *Desmodium eleguns* | 15 | | | | | | | | | | | | | | | | 5 | | | | 7 | | 3 | | |
| 7. *Millettia nitida* | 6 | | 2 | | | | | | 4 | | | | | | | | | | | | | | | | |
| 8. *M. pachycarpa* | 140 | 3 | 12 | | | 9 | 3 | | 18 | 2 | 3 | 7 | 6 | 39 | 6 | | | | 11 | 2 | | | 9 | 6 | 4 |
| 9. *M. tsui* | 2 | | | | | | | | | | | | | 2 | | | | | | | | | | | |
| 10. *Pueraria thunbergiana* | 7 | | | | | | | | | | | | | | 7 | | | | | | | | | | |
| PENTAPHYLACACEAE (13 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Pentaphylax euryoides* | 13 | | | | | | | | | | 10 | 3 | | | | | | | | | | | | | |
| RHAMNACEAE (13 indv., 3 spp., 2 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Rhamnus leptophylla* | 2 | | | | | | | | | | | | | | | | | | | 2 | | | | | |
| 2. *Sageretia hamosa* | 3 | | | | | | | | | | | | | | | | | | | | 3 | | | | |
| 3. *S. theejans* | 8 | | | | | | | | | | 3 | | | | 1 | | 1 | | | | | | 3 | | |
| ROSACEAE (4 indv., 2 spp., 2 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Prumus persica* | 2 | | | | | | | | | | | | | | | | | 1 | | | 1 | | | | |
| 2. *Pyrus calleryana* | 2 | | 1 | | | | | | | | | | | 1 | | | | | | | | | | | |

**Appendix A** (continued-5)

| | | LLI1 | LLI4 | LYE | LY3 | LGT | LW | LLI2 | LLI3 | LY1 | LY2 | LYG | LLGQ | LGQ | LB | LGS1 | LGS2 | LGS3 | LGS4 | LWG | LL | LH | LN | LLN | LG |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| RUBIACEAE (125 indv., 4 spp., 4 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Adina racemosa* | 61 | 8 | | 1 | 5 | | 3 | | | | 2 | | | | | | | 1 | | 8 | 20 | 5 | 3 | | 5 |
| 2. *Lasianthus chinensis* | 21 | | | | | | | | | | | | | | | | | | | | 12 | 9 | | | |
| 3. *Randia spinosa* | 42 | | | | | 1 | | | 13 | 9 | | 2 | 2 | 4 | | | | | | 4 | | | 4 | | 3 |
| 4. *Tarenna depauperata* | 1 | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| RUTACEAE (409 indv., 6 spp., 4 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Clausena dunniana var. henryi* | 8 | | | | | | | | | 2 | | | | | | | | 3 | | 1 | | | | | 2 |
| 2. *C. emarginata* | 3 | | | | | | | | | | | | | | | | | | | | | | | 3 | |
| 3. *C. excavata* | 277 | 7 | | | 3 | | 20 | 13 | 33 | 3 | 32 | 25 | | 18 | 7 | | | 7 | 4 | 11 | 17 | 7 | 32 | 6 | 32 |
| 4. *Glycosmis citrifolia* | 16 | 5 | | | | | | | 2 | 2 | 5 | | | | | | | | | 2 | | | | | |
| 5. *Murraya paniculata* | 103 | 15 | | | | 2 | 5 | | 9 | | | | 3 | 13 | | | 1 | | 5 | 20 | 8 | 14 | | 3 | 5 |
| 6. *Zanthoxylum dissioides* | 2 | | | | | | | | | | | | | | | | | | | | 2 | | | | |
| SAPINDACEAE (207 indv., 4 spp., 4 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Amesiodendron chinense* | 57 | | | 8 | 2 | 6 | 9 | | | | 1 | | | 2 | 2 | | | | 11 | | 9 | 2 | | | 5 |
| 2. *Delavaya yunnanensis* | 41 | | | 6 | 4 | | | | | 2 | 11 | 5 | | | | | | | | | | 13 | | | |
| 3. *Litchi chinensis* | 105 | | | 29 | | 31 | | | | | | 2 | 3 | 15 | 1 | | | | 3 | | 7 | 1 | 1 | 10 | 2 |
| 4. *Sapindus mukoross* | 4 | | | | | | | | | | | | | | | | | | 4 | | | | | | |
| SIMARUBACEAE (10 indv., 2 spp., 2 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Brucea mollis var. tonkinensis* | 8 | | | | | | | | | | | | | | | | | | 4 | 4 | | | | | |
| 2. *Picrasma quassioides* | 3 | | | | | | | | | | | | | 1 | | | | | 1 | 1 | | | | | |
| SOLANACEAE (159 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Solanum verbascifolium* | 159 | | | | | | 14 | | 24 | 26 | 4 | 5 | 5 | 21 | 9 | 1 | | 4 | 4 | 4 | 19 | 9 | | | 10 |
| STERCULIACEAE (643 indv., 4 spp., 2 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Pterospermum heterophyllum* | 74 | 5 | 2 | 26 | | | 1 | | | | | 1 | | 8 | | | | | | 4 | 18 | 7 | | | 2 |
| 2. *Sterculia euosma* | 558 | 18 | 21 | 5 | | 19 | 3 | 5 | 39 | | 4 | 16 | 8 | 59 | 2 | 7 | 14 | 11 | 33 | 74 | 98 | 32 | 16 | 30 | 44 |
| 3. *S. lanceolata* | 16 | | | | | | | | | | | | | | | | | | | | 16 | | | | |
| 4. *S. nobilis* | 39 | | | | | | | | 1 | | | | | 1 | | | | | 2 | 1 | 34 | | | | |
| STYRACACEAE (1 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Styrax suberifolia* | 1 | | | | | | | | | | | | | 1 | | | | | | | | | | | |
| THEACEAE (2 indv., 1 sp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Camellia longgangensis* | 2 | | | | | | | | 2 | | | | | | | | | | | | | | | | |
| TILIACEAE (255 indv., 3 spp., 3 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Burretiodendron esquirolii* | 4 | | | | | | | | | | | | | | | | | | | | 4 | | | | |

**Appendix A** (continued-6)

| | | LLI1 | LLI4 | LYE | LY3 | LGT | LW | LLI2 | LLI3 | LY1 | LY2 | LYG | LLGQ | LGQ | LB | LGS1 | LGS2 | LGS3 | LGS4 | LWG | LL | LH | LN | LLN | LG |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2. *Grewia biloba* | 246 | | | | | 1 | | 5 | 2 | 1 | 1 | | 3 | 25 | 3 | 11 | 11 | 15 | 11 | 10 | 4 | 65 | 48 | 27 | 3 |
| 3. *Microcos paniculata* | 5 | | | | | | | | | | | | | | | | | | | | 5 | | | | |
| ULMACEAE (804 indv., 5 spp., 3 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Celtis austro-sinensis* | 30 | | | 5 | | | | | 6 | | | | | 5 | | | | | | 4 | 1 | 1 | | 4 | 4 |
| 2. *C. philippinensis* | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | |
| 3. *C. sinensis* | 39 | 3 | | 2 | | | | | 5 | | 2 | | | 1 | | | | 1 | | 7 | 6 | 1 | 7 | 3 | 1 |
| 4. *Pteroceltis tatarinowii* | 772 | 12 | | 2 | | | 54 | | 23 | 5 | 14 | 10 | | 61 | 12 | | 35 | 32 | 4 | 60 | 218 | 127 | 27 | 27 | 49 |
| 5. *Trema orientalis* | 15 | | | | | | 5 | | | | | | | | | | | | | | | | 3 | 7 | |
| URTICACEAE (115 indv., 2 spp., 1 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Debregeasia edulis* | 113 | 2 | | 2 | | 4 | | | 4 | | | 15 | | 18 | 13 | | | 7 | 4 | 14 | 5 | 4 | | 3 | 18 |
| 2. *D. longifolia* | 2 | | | | | | | | 2 | | | | | | | | | | | | | | | | |
| VERBENACEAE (285 indv., 6 spp., 4 gen.) | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1. *Callicarpa longissima* | 3 | | | | | | | | | | | | | | | | | 1 | | | 2 | | | | |
| 2. *C. macrophylla* | 9 | | | | | | | | | | | 2 | | | | | | 4 | 3 | | | | | | |
| 3. *Clerodendron fragrans* | 112 | | | | | | 3 | | | | | 8 | | 58 | | | | 1 | | | 3 | 1 | | 38 | |
| 4. *Premna fulva* | 26 | | | | | | 4 | 2 | | | 2 | | | | 2 | | 3 | 1 | 2 | 5 | | | | 3 | 2 |
| 5. *Vitex negundo* | 7 | | | | | | | | | | | | | | 2 | 5 | | | | | | | | | |
| 6. *V. quinata* | 130 | 9 | | 1 | | 4 | | | 9 | 10 | | 5 | 12 | 2 | | | 4 | | 2 | 18 | 12 | 5 | 20 | 10 | 7 |

| | |
|---|---|
| OVERALL TOTAL | 13204 |
| Number of Species: | 164 |
| Number of Genera: | 112 |
| Number of Families: | 48 |
| Ratio of indv/area (ha): | 1138 |
| Ratio of Spp/area (ha): | 73 spp/ha (see Fig. 2-7) |
| Ratio of indv/spp: | 80.51 |
| Ratio of spp/gen.: | 1.464 |
| Ratio of spp/fam.: | 3.417 |

Appendix B Records of activities from each group (original data)

| GA1 | Date | Feeding | Resting | Moving | Grooming | Playing | Others | Total |
|---|---|---|---|---|---|---|---|---|
| | 97.09.22. | 6 | 11 | 3 | 0 | 0 | 0 | 20 |
| | 97.09.24. | 5 | 6 | 1 | 4 | 4 | 0 | 20 |
| | 97.10.10. | 19 | 82 | 11 | 18 | 12 | 1 | 143 |
| | 97.10.11. | 1 | 1 | 1 | 0 | 0 | 0 | 3 |
| | 97.10.22. | 0 | 24 | 1 | 6 | 0 | 0 | 31 |
| | 97.10.24. | 1 | 5 | 2 | 0 | 0 | 0 | 8 |
| | 97.10.28. | 1 | 3 | 0 | 0 | 0 | 0 | 4 |
| | 97.11.23. | 2 | 12 | 0 | 6 | 0 | 0 | 20 |
| | 97.11.25. | 0 | 2 | 1 | 0 | 0 | 0 | 3 |
| | 97.12.28. | 2 | 2 | 1 | 0 | 0 | 0 | 5 |
| | 98.01.10. | 1 | 4 | 2 | 0 | 0 | 0 | 7 |
| | 98.01.22. | 3 | 1 | 1 | 0 | 0 | 0 | 5 |
| | 98.02.17. | 0 | 6 | 0 | 10 | 0 | 0 | 16 |
| | 98.02.19. | 5 | 15 | 2 | 12 | 4 | 0 | 38 |
| | 98.03.06. | 4 | 14 | 4 | 10 | 0 | 0 | 32 |
| | 98.03.25. | 0 | 14 | 0 | 10 | 0 | 0 | 24 |
| | 98.04.19. | 5 | 20 | 2 | 0 | 0 | 0 | 27 |
| | 98.07.08. | 2 | 1 | 0 | 0 | 0 | 0 | 3 |
| | 98.07.28. | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| overall 19 days | | 57 | 225 | 32 | 76 | 20 | 1 | 411 |
| GA2 | 97.09.22. | 0 | 4 | 0 | 0 | 0 | 0 | 4 |
| | 97.10.12. | 2 | 17 | 10 | 0 | 3 | 0 | 32 |
| | 97.10.15. | 1 | 9 | 4 | 2 | 0 | 0 | 16 |
| | 97.11.19. | 2 | 60 | 8 | 26 | 2 | 0 | 98 |
| | 97.11.26. | 0 | 4 | 2 | 12 | 0 | 0 | 18 |
| | 98.03.04. | 16 | 46 | 8 | 11 | 0 | 0 | 81 |
| | 98.03.25. | 7 | 36 | 7 | 13 | 0 | 0 | 63 |
| | 98.03.29. | 3 | 9 | 2 | 4 | 0 | 0 | 18 |
| | 98.04.10. | 3 | 23 | 6 | 0 | 0 | 1 | 33 |
| | 98.04.19. | 12 | 17 | 12 | 2 | 0 | 0 | 43 |
| | 98.05.22. | 9 | 24 | 8 | 15 | 0 | 0 | 56 |
| | 98.05.25. | 4 | 23 | 8 | 0 | 0 | 0 | 35 |
| | 98.05.31. | 4 | 42 | 3 | 22 | 2 | 0 | 73 |
| | 98.06.03. | 1 | 9 | 1 | 0 | 0 | 0 | 11 |
| | 98.06.13. | 3 | 5 | 4 | 2 | 0 | 0 | 14 |
| | 98.06.27. | 0 | 1 | 1 | 0 | 0 | 0 | 2 |
| | 98.07.23. | 1 | 23 | 6 | 6 | 0 | 2 | 38 |
| | 98.07.27 | 1 | 21 | 3 | 18 | 0 | 0 | 43 |
| | 98.08.26. | 5 | 8 | 2 | 0 | 0 | 0 | 15 |
| | 98.09.08. | 4 | 21 | 3 | 12 | 0 | 0 | 40 |
| | 98.09.12. | 7 | 20 | 3 | 2 | 0 | 0 | 32 |
| overall 21 days | | 85 | 422 | 101 | 147 | 7 | 3 | 765 |
| GA3 | 97.10.30. | 0 | 7 | 1 | 0 | 0 | 3 | 11 |
| | 97.11.16. | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| | 97.11.25. | 0 | 15 | 1 | 0 | 0 | 0 | 16 |
| | 97.11.27. | 1 | 98 | 23 | 18 | 1 | 0 | 141 |
| | 97.12.04. | 0 | 26 | 8 | 2 | 1 | 0 | 37 |
| | 97.12.09. | 1 | 26 | 13 | 0 | 2 | 3 | 45 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 97.12.28. | 10 | 56 | 25 | 8 | 8 | 1 | 108 |
| | 97.12.30. | 1 | 101 | 22 | 36 | 12 | 3 | 175 |
| | 98.01.23. | 10 | 84 | 34 | 8 | 6 | 0 | 142 |
| | 98.02.18. | 5 | 18 | 24 | 0 | 3 | 0 | 50 |
| | 98.02.22. | 1 | 34 | 18 | 8 | 5 | 0 | 66 |
| | 98.02.26. | 4 | 75 | 49 | 12 | 18 | 3 | 161 |
| | 98.03.01. | 8 | 59 | 17 | 4 | 3 | 1 | 92 |
| | 98.03.03. | 9 | 79 | 15 | 0 | 2 | 0 | 105 |
| | 98.03.11. | 25 | 35 | 11 | 7 | 11 | 0 | 89 |
| | 98.03.17. | 4 | 41 | 12 | 22 | 11 | 0 | 90 |
| | 98.04.05. | 19 | 157 | 42 | 46 | 27 | 4 | 295 |
| | 98.04.10. | 5 | 5 | 4 | 0 | 7 | 0 | 21 |
| | 98.04.18. | 1 | 11 | 5 | 4 | 5 | 0 | 26 |
| | 98.04.20. | 29 | 63 | 42 | 12 | 16 | 0 | 162 |
| | 98.04.22. | 0 | 62 | 19 | 14 | 16 | 0 | 111 |
| | 98.05.21. | 9 | 39 | 9 | 6 | 14 | 0 | 77 |
| | 98.05.23. | 3 | 78 | 14 | 8 | 4 | 1 | 108 |
| | 98.05.26. | 25 | 100 | 22 | 28 | 18 | 5 | 198 |
| | 98.06.02. | 8 | 6 | 22 | 0 | 6 | 0 | 42 |
| | 98.06.08. | 1 | 87 | 18 | 18 | 22 | 1 | 147 |
| | 98.06.30. | 7 | 28 | 18 | 16 | 6 | 0 | 75 |
| | 98.07.03. | 12 | 94 | 15 | 10 | 4 | 0 | 135 |
| | 98.07.21. | 29 | 62 | 25 | 22 | 8 | 4 | 150 |
| | 98.07.26. | 5 | 13 | 7 | 0 | 4 | 0 | 29 |
| | 98.08.22. | 13 | 48 | 17 | 2 | 9 | 0 | 89 |
| | 98.08.25. | 22 | 51 | 23 | 4 | 11 | 5 | 116 |
| | 98.08.26. | 8 | 4 | 6 | 0 | 4 | 0 | 22 |
| | 98.08.30. | 26 | 153 | 46 | 44 | 17 | 5 | 291 |
| | 98.09.01. | 6 | 25 | 14 | 6 | 10 | 1 | 62 |
| | 98.09.04. | 32 | 56 | 20 | 28 | 17 | 1 | 154 |
| | 98.09.07. | 14 | 75 | 17 | 16 | 15 | 1 | 138 |
| | 98.09.09. | 15 | 44 | 16 | 10 | 23 | 2 | 110 |
| | 98.09.12. | 3 | 16 | 5 | 6 | 2 | 0 | 32 |
| overall | 39 days | 371 | 2032 | 699 | 425 | 348 | 44 | 3919 |
| GA4 | 97.11.08. | 8 | 45 | 9 | 44 | 2 | 1 | 109 |
| | 97.11.21. | 49 | 12 | 5 | 4 | 0 | 0 | 70 |
| | 97.11.23. | 21 | 26 | 8 | 14 | 0 | 1 | 70 |
| | 97.11.24. | 11 | 74 | 14 | 30 | 0 | 0 | 129 |
| | 97.11.27. | 14 | 32 | 8 | 24 | 0 | 0 | 78 |
| | 97.11.30. | 4 | 32 | 18 | 4 | 0 | 2 | 60 |
| | 97.12.05. | 23 | 42 | 9 | 22 | 6 | 6 | 108 |
| | 97.12.07. | 5 | 6 | 8 | 4 | 2 | 0 | 25 |
| | 97.12.08. | 10 | 10 | 7 | 6 | 0 | 0 | 33 |
| | 97.12.10. | 6 | 5 | 12 | 2 | 0 | 1 | 26 |
| | 97.12.18. | 9 | 38 | 13 | 26 | 0 | 0 | 86 |
| | 97.12.22. | 5 | 17 | 6 | 6 | 0 | 0 | 34 |
| | 97.12.25. | 0 | 39 | 7 | 26 | 0 | 0 | 72 |
| | 97.12.28. | 0 | 25 | 14 | 20 | 0 | 0 | 59 |
| | 97.12.30. | 2 | 18 | 12 | 28 | 0 | 4 | 64 |
| | 98.01.03. | 12 | 48 | 13 | 34 | 0 | 0 | 107 |
| | 98.01.08. | 1 | 25 | 3 | 14 | 0 | 0 | 43 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 98.01.10. | 5 | 52 | 20 | 20 | 0 | 0 | 97 |
| | 98.01.16. | 0 | 12 | 0 | 10 | 0 | 0 | 22 |
| | 98.02.12. | 13 | 18 | 6 | 2 | 0 | 0 | 39 |
| | 98.02.14. | 8 | 21 | 5 | 2 | 0 | 0 | 36 |
| | 98.02.17. | 2 | 18 | 6 | 2 | 0 | 0 | 28 |
| | 98.02.19. | 17 | 46 | 7 | 34 | 4 | 0 | 108 |
| | 98.02.21. | 7 | 54 | 12 | 12 | 0 | 2 | 87 |
| | 98.02.25. | 1 | 10 | 0 | 6 | 0 | 0 | 17 |
| overall | 25 days | 233 | 725 | 222 | 396 | 14 | 17 | 1607 |
| GA4' | 97.12.23. | 2 | 3 | 3 | 3 | 0 | 0 | 11 |
| | 98.03.21. | 0 | 30 | 3 | 4 | 0 | 0 | 37 |
| | 98.03.31. | 21 | 54 | 11 | 14 | 6 | 0 | 106 |
| overall | 3 days | 23 | 87 | 17 | 21 | 6 | 0 | 154 |
| GA4" | 98.05.15. | 0 | 11 | 8 | 4 | 4 | 1 | 28 |
| | 98.05.18. | 1 | 20 | 5 | 2 | 0 | 0 | 28 |
| | 98.05.21. | 7 | 11 | 0 | 2 | 2 | 0 | 22 |
| | 98.05.24. | 7 | 33 | 14 | 23 | 8 | 0 | 85 |
| | 98.05.26. | 6 | 31 | 15 | 2 | 2 | 0 | 56 |
| | 98.05.28. | 6 | 3 | 2 | 6 | 0 | 0 | 17 |
| | 98.05.29. | 4 | 14 | 11 | 8 | 2 | 3 | 42 |
| | 98.06.03. | 3 | 12 | 6 | 0 | 0 | 0 | 21 |
| | 98.06.13. | 20 | 22 | 8 | 4 | 1 | 1 | 56 |
| | 98.07.07. | 19 | 19 | 9 | 6 | 8 | 0 | 61 |
| | 98.07.31. | 9 | 5 | 5 | 2 | 0 | 0 | 21 |
| | 98.08.28. | 1 | 0 | 3 | 0 | 0 | 0 | 4 |
| | 98.08.30. | 16 | 37 | 17 | 18 | 10 | 0 | 98 |
| | 98.09.05. | 6 | 31 | 19 | 4 | 0 | 1 | 61 |
| | 98.09.08. | 6 | 2 | 3 | 6 | 0 | 0 | 17 |
| overall | 15 days | 111 | 251 | 125 | 87 | 37 | 6 | 617 |
| GA5 | 97.10.31. | 0 | 8 | 1 | 0 | 0 | 0 | 9 |
| | 97.11.16. | 0 | 3 | 5 | 0 | 0 | 0 | 8 |
| | 97.12.30. | 0 | 6 | 6 | 0 | 0 | 0 | 12 |
| | 98.01.21. | 17 | 59 | 24 | 6 | 5 | 1 | 112 |
| | 98.01.22. | 1 | 22 | 7 | 4 | 2 | 0 | 36 |
| | 98.02.17. | 12 | 35 | 28 | 4 | 6 | 0 | 85 |
| | 98.02.24. | 2 | 11 | 4 | 0 | 2 | 0 | 19 |
| | 98.02.26. | 0 | 4 | 5 | 0 | 0 | 1 | 10 |
| | 98.03.03. | 0 | 11 | 7 | 6 | 5 | 0 | 29 |
| | 98.03.06. | 2 | 71 | 6 | 12 | 7 | 1 | 99 |
| | 98.03.08. | 0 | 10 | 3 | 2 | 4 | 0 | 19 |
| | 98.03.23. | 5 | 61 | 5 | 8 | 8 | 0 | 87 |
| | 98.03.26. | 16 | 42 | 15 | 0 | 10 | 0 | 83 |
| overall | 13 days | 55 | 343 | 116 | 42 | 49 | 3 | 608 |
| GA6 | 97.12.04. | 2 | 19 | 11 | 0 | 2 | 3 | 37 |
| | 97.12.23. | 0 | 7 | 4 | 0 | 2 | 0 | 13 |
| | 98.05.19. | 1 | 38 | 8 | 0 | 10 | 0 | 57 |
| | 98.06.02. | 0 | 11 | 2 | 0 | 2 | 0 | 15 |
| overall | 4 days | 3 | 75 | 25 | 0 | 16 | 3 | 122 |
| GA7 | 98.01.17. | 9 | 53 | 13 | 6 | 0 | 0 | 81 |
| | 98.02.15. | 10 | 16 | 16 | 4 | 0 | 0 | 46 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 98.02.20. | 9 | 52 | 14 | 23 | 0 | 0 | 98 |
| | 98.02.22. | 18 | 25 | 12 | 16 | 0 | 0 | 71 |
| | 98.02.25. | 9 | 50 | 12 | 13 | 0 | 0 | 84 |
| | 98.04.08. | 6 | 29 | 5 | 2 | 0 | 0 | 42 |
| | 98.05.20. | 4 | 32 | 6 | 10 | 2 | 0 | 54 |
| | 98.05.30. | 27 | 57 | 21 | 49 | 0 | 0 | 154 |
| | 98.06.28. | 5 | 8 | 1 | 0 | 0 | 0 | 14 |
| | 98.07.26. | 1 | 35 | 7 | 4 | 0 | 0 | 47 |
| | 98.08.24 | 5 | 6 | 6 | 2 | 0 | 0 | 19 |
| overall | 11 days | 103 | 363 | 113 | 129 | 2 | 0 | 710 |
| GA8 | 97.12.31. | 10 | 21 | 12 | 6 | 0 | 0 | 49 |
| | 98.02.10. | 2 | 33 | 6 | 24 | 0 | 0 | 65 |
| | 98.02.20. | 7 | 17 | 9 | 0 | 0 | 0 | 33 |
| | 98.02.22. | 0 | 6 | 4 | 2 | 0 | 0 | 12 |
| | 98.02.25. | 16 | 41 | 14 | 8 | 0 | 0 | 79 |
| | 98.03.05. | 15 | 25 | 12 | 0 | 0 | 0 | 52 |
| | 98.03.08. | 4 | 3 | 2 | 0 | 0 | 0 | 9 |
| | 98.03.24. | 0 | 0 | 4 | 0 | 0 | 0 | 4 |
| | 98.04.01. | 11 | 28 | 9 | 7 | 2 | 0 | 57 |
| | 98.04.04. | 12 | 44 | 11 | 8 | 7 | 1 | 83 |
| | 98.04.06. | 2 | 12 | 3 | 2 | 0 | 0 | 19 |
| | 98.04.11. | 23 | 22 | 8 | 0 | 3 | 0 | 56 |
| | 98.04.14. | 11 | 15 | 9 | 2 | 0 | 0 | 37 |
| | 98.04.19. | 16 | 47 | 11 | 4 | 2 | 0 | 80 |
| | 98.05.14. | 10 | 8 | 7 | 2 | 0 | 7 | 34 |
| | 98.05.15. | 17 | 16 | 8 | 0 | 0 | 0 | 41 |
| | 98.05.18. | 0 | 8 | 3 | 2 | 0 | 0 | 13 |
| | 98.05.25. | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| | 98.05.27. | 9 | 20 | 13 | 2 | 2 | 0 | 46 |
| | 98.05.29. | 15 | 30 | 11 | 14 | 0 | 0 | 70 |
| | 98.05.31. | 4 | 3 | 7 | 2 | 0 | 0 | 16 |
| | 98.06.02. | 3 | 4 | 5 | 0 | 0 | 0 | 12 |
| | 98.06.05. | 2 | 45 | 3 | 15 | 0 | 0 | 65 |
| | 98.06.09. | 7 | 28 | 9 | 0 | 2 | 5 | 51 |
| | 98.06.27. | 9 | 9 | 6 | 4 | 0 | 0 | 28 |
| | 98.06.30. | 13 | 12 | 5 | 4 | 0 | 0 | 34 |
| | 98.07.10. | 5 | 8 | 5 | 8 | 0 | 0 | 26 |
| | 98.07.12. | 2 | 7 | 0 | 2 | 0 | 0 | 11 |
| | 98.07.17. | 3 | 17 | 0 | 6 | 0 | 0 | 26 |
| | 98.07.21. | 3 | 13 | 5 | 2 | 0 | 0 | 23 |
| | 98.07.24. | 5 | 16 | 6 | 4 | 0 | 1 | 32 |
| | 98.07.26. | 2 | 4 | 4 | 0 | 0 | 0 | 10 |
| | 98.08.23. | 15 | 30 | 10 | 6 | 0 | 0 | 61 |
| | 98.08.27. | 7 | 3 | 0 | 0 | 0 | 0 | 10 |
| | 98.08.30. | 7 | 20 | 4 | 14 | 0 | 0 | 45 |
| | 98.09.03. | 16 | 5 | 7 | 13 | 3 | 0 | 44 |
| | 98.09.08. | 3 | 4 | 2 | 0 | 5 | 0 | 14 |
| overall | 37 days | 286 | 627 | 234 | 163 | 26 | 14 | 1350 |
| GAF | 98.07.13. | 1 | 8 | 4 | 0 | 0 | 0 | 13 |
| | 98.07.28. | 5 | 16 | 2 | 12 | 0 | 4 | 39 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 98.08.25. | 0 | 12 | 1 | 14 | 0 | 0 | 27 |
| | 98.08.27. | 10 | 8 | 6 | 0 | 0 | 2 | 26 |
| overall | 4 days | 16 | 44 | 13 | 26 | 0 | 6 | 105 |
| GAGL | 98.01.23. | 2 | 21 | 2 | 4 | 0 | 0 | 29 |
| | 98.07.12. | 4 | 12 | 3 | 2 | 0 | 1 | 22 |
| | 98.07.23. | 4 | 4 | 0 | 0 | 0 | 0 | 8 |
| overall | 3 days | 10 | 37 | 5 | 6 | 0 | 1 | 59 |
| GALN | 97.11.21. | 8 | 12 | 5 | 0 | 0 | 0 | 25 |
| | 98.04.20. | 10 | 64 | 12 | 4 | 23 | 0 | 113 |
| | 98.06.04. | 5 | 13 | 3 | 2 | 12 | 2 | 37 |
| overall | 3 days | 23 | 89 | 20 | 6 | 35 | 2 | 175 |
| unid. groups | | | | | | | | |
| Solo1 | 97.09.29. | 1 | 2 | 0 | 0 | 0 | 0 | 3 |
| Solo2 | 97.10.28. | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| | 97.10.30. | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| overall | 2 days | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| Unid.1 | 97.10.23. | 7 | 37 | 4 | 0 | 0 | 0 | 48 |
| | 98.01.17. | 1 | 2 | 2 | 0 | 0 | 0 | 5 |
| overall | 2 days | 8 | 39 | 6 | 0 | 0 | 0 | 53 |
| Unid.2 | 97.10.30. | 1 | 4 | 0 | 0 | 0 | 0 | 5 |
| | 98.07.29. | 0 | 4 | 1 | 4 | 0 | 0 | 9 |
| overall | 2 days | 1 | 8 | 1 | 4 | 0 | 0 | 14 |
| Unid.3 | 97.11.19. | 2 | 16 | 10 | 2 | 0 | 0 | 30 |
| Unid.4 | 97.12.07. | 2 | 12 | 0 | 2 | 0 | 0 | 16 |
| Unid.5 | 98.01.17. | 0 | 19 | 2 | 0 | 0 | 0 | 21 |
| Unid.6 | 98.01.18. | 1 | 27 | 5 | 12 | 0 | 1 | 46 |
| | 98.01.20. | 4 | 45 | 4 | 2 | 0 | 0 | 55 |
| overall | 2 days | 5 | 72 | 9 | 14 | 0 | 1 | 101 |
| Unid.7 | 98.01.18. | 1 | 0 | 1 | 0 | 0 | 0 | 2 |
| Unid.8 | 98.02.24. | 1 | 14 | 3 | 0 | 0 | 0 | 18 |
| Unid.9 | 98.03.24. | 1 | 18 | 1 | 4 | 0 | 0 | 24 |
| Unid.10 | 98.05.17. | 4 | 21 | 3 | 0 | 0 | 0 | 28 |
| Unid.11 | 98.06.03. | 6 | 7 | 2 | 0 | 0 | 0 | 15 |
| Unid.12 | 98.06.07. | 3 | 8 | 6 | 0 | 5 | 0 | 22 |
| Unid.13 | 98.08.29. | 8 | 17 | 4 | 4 | 0 | 1 | 34 |
| | 98.09.11 | 5 | 13 | 3 | 8 | 0 | 0 | 29 |
| overall | 2 days | 13 | 30 | 7 | 12 | 0 | 1 | 63 |

Appendix C Feeding records on plant species

| groups | months | Species | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GA1 | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 31 | 32 | 34 |
| | 97.09. | | | | | | 1 | | | | | | 1 | | | | | | | | | 5 | | | | | | | | | 1 | |
| | 97.10. | 2 | | | | 1 | | | | | | | 2 | | | | 3 | 1 | | | | | | 1 | 1 | | | | 2 | | | |
| | 97.11. | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | 97.12. | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | 1 | | |
| | 98.01. | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| | 98.02. | 1 | | | | | | | | | | | | | | | | | | | | | | | | 3 | | | | | 1 | |
| | 98.03. | | | | | | | | | | 1 | | | | | | | | | | 1 | | | 1 | | | | | 1 | | | |
| | 98.04. | | | | | | | | | | | | | | | | | | | | | | | | | 2 | | | 1 | | | |
| | 98.07. | | 1 | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | |
| GA2 | 97.10. | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| | 97.11. | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | |
| | 98.03. | 1 | 3 | | | | | | | | | | | | | | | | | | | | | | | 13 | | | | | 1 | |
| | 98.04. | 2 | | | | 1 | | | | | | | | 1 | | | | | 1 | | | 1 | | | | 2 | | | | | 5 | |
| | 98.05. | 5 | | 1 | 1 | 1 | | | | 1 | | | | 2 | | | | 1 | 1 | | | | | | | 1 | | 1 | | | | |
| | 98.06. | | 1 | | | | | | | | | | | | | | | | | | | 2 | | | | | 1 | | | | | |
| | 98.07. | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | |
| | 98.08. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | 98.09. | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 | | |
| GA3 | 97.11. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| | 97.12. | 2 | 5 | | | | | | 2 | | | | | | | | | | | | | | | 1 | | | | | | | | |
| | 98.01. | 1 | 1 | 4 | | | | | | | | | | | | | | | | | | | 1 | | | 1 | | | | | 2 | |
| | 98.02. | 1 | | | | | | | 1 | | | | | | | | | | | | 1 | | | 1 | | 2 | | | | 2 | 1 | |
| | 98.03. | 3 | 6 | | | 1 | | 1 | 2 | | 2 | | | 11 | | | | 1 | | | | | | 1 | | 4 | | | | 4 | 1 | |
| | 98.04. | 2 | 10 | 1 | | 2 | | | 1 | | | | 3 | 1 | | | | | | | 1 | 1 | 1 | | | 6 | | | | 1 | 10 | 1 |
| | 98.05. | 7 | 7 | 1 | | 1 | | 1 | | | | | | | | | 2 | 4 | | | | | | | | 4 | | 2 | | 2 | | |
| | 98.06. | 2 | 1 | | | | | | | 1 | 2 | 1 | | | | | | | | | 1 | | | | | | | 1 | | | 3 | |
| | 98.07. | 2 | 9 | | | 1 | | | | | 2 | | | | | | | | | | | 2 | | | | 12 | | | 2 | 1 | 1 | 1 |
| | 98.08. | 3 | 6 | 1 | | 1 | 1 | | | | 4 | 1 | 3 | | | | | | | | | | | 1 | 2 | 4 | | 1 | 4 | 2 | 5 | |
| | 98.09. | 3 | 14 | 1 | | 1 | | | | 1 | | 1 | | | | | 4 | | | | | 4 | | | | 7 | | | | | 1 | |
| GA4 | 97.11. | 2 | 2 | | | | | | | | | | | | | | | | | 41 | | 2 | | 1 | | 48 | | | | | 1 | |
| | 97.12. | 1 | | | 2 | 3 | | | | | | | | | | | 2 | | | 9 | | 2 | | 6 | | 19 | | 1 | 5 | 1 | | 1 |

Appendix C (continued)

| groups | months | Species | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 31 | 32 | 34 |
| GA4 | 98.01. | | 1 | | | 5 | | | | | | | | | | | | | | | | | | | | 10 | | | 2 | | | |
| | 98.02. | 9 | | 2 | | 3 | | 1 | 1 | 1 | | | | | | 1 | | | | 10 | 2 | | | 3 | | 6 | | 1 | 4 | 1 | 1 | 1 |
| GA4' | 97.12. | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | |
| | 98.03. | 3 | 4 | | | 1 | 2 | | 1 | | 2 | | | | | | | | | | | 1 | | | | | | | | | 4 | |
| GA4'' | 98.05. | 5 | 3 | 1 | | 2 | | | 1 | 1 | | | | 2 | | | | | | | 1 | 4 | | | 1 | 6 | | 2 | 1 | | | |
| | 98.06. | 6 | 3 | | | 3 | | | | | | | | | | | 1 | | 1 | | | | | 1 | | | | 1 | 1 | 1 | 5 | |
| | 98.07. | 3 | 7 | | | 1 | | | | 2 | | | | | | | 3 | | 1 | | | 1 | | | | 3 | | | 2 | | | |
| | 98.08. | | 6 | | | 1 | | | | | | | | | | | | | 1 | | | | 1 | | | 1 | | 1 | | | | |
| | 98.09. | | 2 | | 1 | 2 | | | | | | | | | | | 2 | | | | | | | | | 1 | | 1 | | | | |
| GA5 | 98.01. | 4 | 1 | 1 | | 2 | 2 | | | | | | 1 | | | | | | | | 1 | | | 1 | | 2 | | | | | | |
| | 98.02. | 2 | | | | 1 | | | | | | | 2 | | | | | | | | | | | 1 | | 7 | | 1 | | | | |
| | 98.03. | | 4 | | | | | | | | | | | | | | | | | | 1 | 6 | | | | 1 | | | | | 9 | |
| GA6 | 97.12. | | | | | | | | | | | | | | | | | | | | | | | | | 2 | | | | | | |
| | 98.05. | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| GA7 | 98.01. | | | 1 | | | | | 1 | | | | | | | | | | | | | | | | | 5 | | 1 | | | | |
| | 98.02. | 1 | | 1 | | 1 | | | 1 | | | | | | | | 2 | | 1 | 7 | 2 | | 1 | 2 | | 20 | | 1 | 3 | 1 | | |
| | 98.04. | | 4 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| | 98.05. | 1 | 3 | 1 | 1 | 3 | | 1 | | | 3 | | | | | | | | | | 3 | | 1 | | | 1 | 1 | | | | 2 | |
| | 98.06. | 1 | 2 | | | | | | | | | | | | | | | | | | | | | | 2 | | | | | | | |
| | 98.07. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | 98.08. | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | |
| GA8 | 97.12. | 2 | 3 | 1 | | | | | | | | | | | | | | | | | | | | 3 | | | | | 1 | | | |
| | 98.02. | 9 | 4 | | | 2 | | | 3 | | | | | | | | | | 1 | | 1 | | | | | | | | | | 1 | 2 |
| | 98.03. | 6 | 2 | | | 1 | | | | | 1 | | 1 | | | | | | | | 1 | | | 1 | | 2 | | 1 | 1 | | 2 | |
| | 98.04. | 6 | 13 | | | | | | | 3 | 3 | | 4 | 1 | | | 1 | | | | 1 | 1 | | | | 2 | | | | 1 | 5 | 1 |
| | 98.05. | 9 | 7 | | | 1 | 1 | | 1 | | 1 | | 9 | | | | 3 | | | | | 3 | | 2 | | 2 | | 5 | | 1 | | |
| | 98.06. | 5 | 3 | | | 3 | | | | | | 1 | | | | | | | 1 | | | 5 | 1 | | 1 | 1 | | 4 | | | 4 | |
| | 98.07. | 2 | | 2 | | | | | | 2 | | | | | | | | | 1 | | | 2 | | | | 5 | | | | | 1 | |
| | 98.08. | 3 | 2 | 1 | | 4 | 1 | | | | 1 | | | 1 | | | 1 | | | | | | | | | | | 2 | | | 1 | |
| | 98.09. | 2 | 2 | | | | | | | | | 1 | 1 | 1 | | | | | | | | 2 | 1 | 1 | 1 | | | 1 | | | 3 | |
| GAGL | 98.01. | | | | | 1 | | 1 | | | | | | | | | | | | | | | | | | | | | | | | |

Appendix C (continued)

| groups | months | Species | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 31 | 32 | 34 |
| GAGL | 98.07. | 1 | | 2 | | 1 | | | | 1 | | | | | | | | | | | | | | | | | | | | | | |
| GALN | 97.11. | 2 | 1 | | | | | | | | | | | | | | | | | | | | | 2 | | 3 | | | | | | |
| | 98.04. | | | | | 1 | | | 1 | | | | | | | | | | | | | | | | | | | | | | 3 | |
| | 98.06. | | 1 | | | | | | | | | | | | | | 2 | | | | | | | | | 1 | | 1 | | | | |
| GAF | 98.07. | | | | | 1 | | | | | | | | 1 | | | | | | | | | | | | 3 | | | | | | |
| | 98.08. | | 3 | | | | | | | | | | | | | | | | | | 1 | 3 | | | 1 | | | 1 | | | 1 | |
| Solo1 | 97.09. | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | |
| Unid.1 | 97.10. | | 2 | | | | | | | | | | | | | | | | | | | | | | | 3 | | | | | | |
| | 98.01. | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | |
| Unid.2 | 97.10. | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | |
| Unid.3 | 97.11. | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | |
| Unid.4 | 97.12. | | 1 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | |
| Unid.6 | 98.01. | | 1 | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | 1 | 1 | |
| Unid.7 | 98.01. | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | |
| Unid.8 | 98.02. | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | |
| Unid.9 | 98.03. | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| Unid.10 | 98.05. | | 1 | | | | | | | | | | | | | | 1 | | 1 | | | | | | | | | | | | | |
| Unid.11 | 98.06. | | | | | | | | | | 3 | 2 | | 1 | | | | | | | | | | | | | | | | | | |
| Unid.12 | 98.06. | | | | | | | | | | | | | | | | | | | | | | | 2 | 1 | | | | | | | |
| Unid.13 | 98.08. | 3 | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| | 98.09. | 1 | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | | | | | | |

Appendix C (continued)

| groups | months | Species | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GA1 | | 35 | 37 | 41 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | Un-id. |
| | 97.09. | 1 | | | | | | | | | | | | | | | | | | | 2 |
| | 97.10. | 4 | | | | | | | | | | | | | | | | | | | 5 |
| | 97.11. | | | | | | | | | | | | | | | | | | | | |
| | 97.12. | | | | | | | | | | | | | | | | | | | | |
| | 98.01. | | | | | | | | | | | | | | | | | | | | 2 |
| | 98.02. | | | | | | | | | | | | | | | | | | | | |
| | 98.03. | | | | | | | | | | | | | | | | | | | | |
| | 98.04. | | | | | | | 1 | | | | | | | | | | | | | 1 |
| | 98.07. | | | | | | | | | | | | | | | | | | | | |
| GA2 | 97.10. | | | | | | | | | | | | | | | | | | | | 1 |
| | 97.11. | 1 | | | | | | | | | | | | | | | | | | | |
| | 98.03. | | | | | 1 | 3 | | | | | | | | | | | | | | 4 |
| | 98.04. | | | 2 | | | | | | | | | | | | | | | | | |
| | 98.05. | 1 | | 1 | | | | | | | | | | | | | | | | | |
| | 98.06. | | | | | | | | | | | | | | | | | | | | |
| | 98.07. | | | | | | | | 1 | | | | | | | | | | | | |
| | 98.08. | | | | | | | | 5 | | | | | | | | | | | | |
| | 98.09. | 1 | | | | | 2 | 1 | 2 | 2 | | | | | | | | | | | |
| GA3 | 97.11. | | | | | | | | | | | | | | | | | | | | |
| | 97.12. | 2 | | | | | | | | | | | | | | | | | | | |
| | 98.01. | | | | | | | | | | | | | | | | | | | | |
| | 98.02. | | | | | | | | | | | | | | | | | | | | 1 |
| | 98.03. | | | | | 4 | | | | | | | | | | | | | | | 5 |
| | 98.04. | 10 | 1 | | | 1 | 1 | | | | | | | | | | | | | | |
| | 98.05. | 5 | 1 | | | | | | | | | | | | | | | | | | |
| | 98.06. | 2 | | | | | | | 2 | | | | | | | | | | | | |
| | 98.07. | 6 | 5 | | | 1 | | | | 1 | | | | | | | | | | | |
| | 98.08. | 9 | | | | 2 | 1 | 1 | 9 | 5 | | 2 | | | | | 1 | | | | |
| | 98.09. | 5 | | 1 | | 5 | | | 5 | | | 6 | 1 | | | 2 | 3 | 2 | 2 | 1 | |
| GA4 | 97.11. | 5 | | | | | | | | | | | | | | | | | | | 5 |
| | 97.12. | | | | | | | | | | | | | | | | | | | | 8 |

Appendix C (continued)

| groups | months | Species | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 35 | 37 | 41 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | Un-id. |
| GA4 | 98.01. | | | | | | | | | | | | | | | | | | | | |
| | 98.02. | | 1 | | | | | | | | | | | | | | | | | | |
| GA4' | 97.12. | | | | | | | | | | | | | | | | | | | | 1 |
| | 98.03. | | | 3 | | | | | | | | | | | | | | | | | |
| GA4" | 98.05. | 1 | | | | | | | | | | | | | | | | | | | |
| | 98.06. | | | | | | | | | | | | | | | | | | | | |
| | 98.07. | | | 4 | | | | | | | 1 | | | | | | | | | | |
| | 98.08. | | | 1 | | 1 | | | 1 | | | | | 1 | 1 | 1 | | | | | |
| | 98.09. | | | | | 1 | | | 1 | | | | | 1 | | | | | | | |
| GA5 | 98.01. | | | | | | | | | | | | | | | | | | | | 3 |
| | 98.02. | | | | | | | | | | | | | | | | | | | | |
| | 98.03. | | | | | 1 | | | | | | | | | | | | | | | 1 |
| GA6 | 97.12. | | | | | | | | | | | | | | | | | | | | |
| | 98.05. | | | | | | | | | | | | | | | | | | | | |
| GA7 | 98.01. | 1 | | | | | | | | | | | | | | | | | | | |
| | 98.02. | | | | | 1 | | | | | | | | | | | | | | | 1 |
| | 98.04. | | | | | | 1 | | | | | | | | | | | | | | |
| | 98.05. | 7 | | | | | 3 | | | | | | | | | | | | | | |
| | 98.06. | | | | | | | | | | | | | | | | | | | | |
| | 98.07. | | | | | | | | 1 | | | | | | | | | | | | |
| | 98.08. | | 2 | | | | | | 1 | 1 | | | | | | | | | | | |
| GA8 | 97.12. | | | | | | | | | | | | | | | | | | | | |
| | 98.02. | | 1 | | 1 | | | | | | | | | | | | | | | | |
| | 98.03. | | | | | | | | | | | | | | | | | | | | |
| | 98.04. | 6 | 1 | 4 | | | 6 | 15 | | | | | | | | | | | | | 1 |
| | 98.05. | 4 | | | 1 | 1 | | | | | | | | | | | | | | | |
| | 98.06. | 1 | 1 | 6 | | | 1 | | | | | | | | | | | | | | |
| | 98.07. | | 1 | 3 | | | 1 | | | | | | | | | | | | | | |
| | 98.08. | 1 | | | | | 1 | 2 | 2 | 3 | | 1 | | | | 2 | | | | | |
| | 98.09. | | | 2 | | | | | | | | | | | | | | 1 | | | |
| GAGL | 98.01. | | | | | | | | | | | | | | | | | | | | |

Appendix C (continued)

| groups | months | Species | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 35 | 37 | 41 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | Un-id. |
| GAGL | 98.07. | | | | | | 1 | | | 2 | | | | | | | | | | | |
| GALN | 97.11. | | | | | | | | | | | | | | | | | | | | |
| | 98.04. | 3 | | | | | 2 | | | | | | | | | | | | | | |
| | 98.06. | | | | | | | | | | | | | | | | | | | | |
| GAF | 98.07. | | | 1 | | | | | | | | | | | | | | | | | |
| | 98.08. | | | | | | | | | | | | | | | | | | | | |
| Solo1 | 97.09. | | | | | | | | | | | | | | | | | | | | |
| Unid.1 | 97.10. | 1 | | | | | | | | | | | | | | | | | | | 1 |
| | 98.01. | | | | | | | | | | | | | | | | | | | | |
| Unid.2 | 97.10. | | | | | | | | | | | | | | | | | | | | |
| Unid.3 | 97.11. | 1 | | | | | | | | | | | | | | | | | | | |
| Unid.4 | 97.12. | | | | | | | | | | | | | | | | | | | | |
| Unid.6 | 98.01. | | | | | | | | | | | | | | | | | | | | 1 |
| Unid.7 | 98.01. | | | | | | | | | | | | | | | | | | | | |
| Unid.8 | 98.02. | | | | | | | | | | | | | | | | | | | | |
| Unid.9 | 98.03. | | | | | | | | | | | | | | | | | | | | |
| Unid.10 | 98.05. | 1 | | | | | | | | | | | | | | | | | | | |
| Unid.11 | 98.06. | | | | | | | | | | | | | | | | | | | | |
| Unid.12 | 98.06. | | | | | | | | | | | | | | | | | | | | |
| Unid.13 | 98.08. | 1 | 1 | | | | | | | 1 | | 1 | | | | | | | | | |
| | 98.09. | | | | | | | | | | | | | | | | 2 | | | | |

Appendix D Feeding records of food items in each langur group.

| | | YL | ML | SL | L | FLBD | OPFL | FL | IMFR | MFR | ST | Seed |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GA1 | 97.09. | 5 | 2 | | | | | | | | | |
| | 97.10. | 15 | 1 | | | | | | | | 1 | |
| | 97.11. | 2 | | | | | | | | | | |
| | 97.12. | | 2 | | | | | | | | | |
| | 98.01. | 2 | | | | | | | | | | |
| | 98.02. | 5 | | | | | | | | | | |
| | 98.03. | 3 | | | | | | | | | 1 | |
| | 98.04. | 1 | | | | | | | 1 | 2 | | |
| | 98.07. | 2 | | | | | | | | | | |
| GA2 | 97.10. | 1 | 1 | 1 | | | | | | | | |
| | 97.11. | | 1 | | 1 | | | | | | | |
| | 98.03. | 23 | | | | | | | | | | |
| | 98.04. | 15 | | | | | | | | | | |
| | 98.05. | 15 | 1 | | | | | | 1 | | | |
| | 98.06. | 2 | 2 | | | | | | | | | |
| | 98.07. | 1 | 1 | | | | | | | | | |
| | 98.08. | 5 | | | | | | | | | | |
| | 98.09. | 10 | 1 | | | | | | | | | |
| GA3 | 97.11. | 1 | | | | | | | | | | |
| | 97.12. | 2 | 9 | | | | | | | | 1 | |
| | 98.01. | 2 | 8 | | | | | | | | | |
| | 98.02. | 9 | | | | | | | | | 1 | |
| | 98.03. | 38 | 5 | | 1 | | | | | | 1 | |
| | 98.04. | 51 | 1 | | 2 | | | | | | | |
| | 98.05. | 30 | 1 | | 6 | | | | | | | |
| | 98.06. | 13 | | | 2 | 1 | | | | | | |
| | 98.07. | 28 | | | 14 | | | | 4 | | | |
| | 98.08. | 58 | 3 | | 3 | 2 | | | | | 1 | 2 |
| | 98.09. | 49 | 3 | | 6 | 5 | 1 | 1 | | | | 5 |
| GA4 | 97.11. | 54 | 8 | | | | | | | 41 | | |
| | 97.12. | 28 | 10 | | | | | | | 9 | 6 | |
| | 98.01. | 15 | 3 | | | | | | | | | |
| | 98.02. | 32 | 3 | | | 10 | | | | | 3 | |
| GA4' | 97.12. | 1 | | | | | | | | | | |
| | 98.03. | 21 | | | | | | | | | | |
| GA4" | 98.05. | 21 | 1 | | 4 | | | | | 5 | | |
| | 98.06. | 18 | 2 | | | | | | 1 | | 1 | 1 |
| | 98.07. | 23 | 2 | | | | | | 2 | 1 | | |
| | 98.08. | 16 | | | | | | | 1 | | | |
| | 98.09. | 8 | | | 2 | | | 1 | | | 1 | |
| GA5 | 98.01. | 5 | 9 | | | | | | | | 1 | |
| | 98.02. | 10 | 3 | | | | | | | | 1 | |
| | 98.03. | 22 | | | 1 | | | | | | | |
| GA6 | 97.12. | 2 | | | | | | | | | | |
| | 98.05. | | | | 1 | | | | | | | |
| GA7 | 98.01. | 8 | 1 | | | | | | | | | |
| | 98.02. | 36 | | | | 7 | | | | | 2 | |
| | 98.04. | 6 | | | | | | | | | | |
| | 98.05. | 23 | 4 | | 4 | | | | | | | |
| | 98.06. | 5 | | | | | | | | | | |
| | 98.07. | 1 | | | | | | | | | | |

Appendix D (*continued*)

| | | YL | ML | SL | L | FLBD | OPFL | FL | IMFR | MFR | ST | Seed |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 98.08. | 3 | | | | | | | 2 | | | |
| GA8 | 97.12. | 3 | 4 | | | | | | | | 3 | |
| | 98.02. | 21 | 3 | | | 1 | | | | | | |
| | 98.03. | 17 | 1 | | | | | | | | 1 | |
| | 98.04. | 58 | | | | | | | 15 | | | |
| | 98.05. | 36 | 7 | | 3 | 1 | 2 | | | | 2 | |
| | 98.06. | 27 | 4 | | 2 | | | | 4 | | | 1 |
| | 98.07. | 15 | 3 | | | | | | 1 | 1 | | |
| | 98.08. | 27 | | | 1 | | | | | | | 1 |
| | 98.09. | 17 | | | 1 | | | | | | 1 | |
| GAGL | 98.01. | 2 | | | | | | | | | | |
| | 98.07. | 8 | | | | | | | | | | |
| GALN | 97.11. | 3 | | | | | | | | 3 | | |
| | 98.04. | 10 | | | | | | | | | | |
| | 98.06. | 3 | | | 2 | | | | | | | |
| GAF | 98.07. | 4 | | | 1 | | | | | | | 1 |
| | 98.08. | 8 | 1 | | 1 | | | | | | | |
| Solo1 | 97.09. | 1 | | | | | | | | | | |
| Unid.1 | 97.10. | 5 | 1 | | | | | | | | | |
| | 98.01. | | 1 | | | | | | | | | |
| Unid.2 | 97.10. | | | | | | | | | | | |
| Unid.3 | 97.11. | 2 | | | | | | | | | | |
| Unid.4 | 97.12. | 1 | 1 | | | | | | | | | |
| Unid.6 | 98.01. | 2 | 2 | | | | | | | | | |
| Unid.7 | 98.01. | 1 | | | | | | | | | | |
| Unid.8 | 98.02. | 1 | | | | | | | | | | |
| Unid.9 | 98.03. | | | | | | 1 | | | | | |
| Unid.10 | 98.05. | 4 | | | | | | | | | | |
| Unid.11 | 98.06. | 3 | | | 3 | | | | | | | |
| Unid.12 | 98.06. | 1 | | | | | | | | | 2 | |
| Unid.13 | 98.08. | 5 | | | 2 | | | | | | | 1 |
| | 98.09. | 5 | | | | | | | | | | |