ECOLOGY AND BEHAVIOUR OF BLACK GIBBONS IN YUNNAN, CHINA

Daoying Lan

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ABSTRACT

This study investigates the behavioural ecology of the black gibbon, *Hylobates concolor*, at research sites with human disturbance in Yunnan province, China. This location is close to the present northern distribution limits of this primate species and genus, and represents sub-tropical Asian biogeography, a transitional position in flora and fauna. It is characterised by marked seasonality, especially in terms of precipitation. Black gibbons live in small family groups; a group of animals mainly consisting of unrelated parents and related offsprings. Group size and composition data of some groups suggested that multi-female groups existed in this gibbon species, which may differentiate this species from other hylobatids.

A detailed climatic analysis revealed that freezing conditions occurred in the study habitats. Temperature variation is obvious both daily and yearly. Vegetation diversity was not as high as in tropical Asia. Monthly phenological sampling of plant species in the habitats of the study groups revealed that these habitats were also distinct in terms of flowering and fruiting patterns. Ripe fruit abundance peaked at the end of wet season and lasted to early dry season, with fruit resources being scarce across the entire study plot during the mid dry season from January to March and April. Fig trees were scarce but not completely absent. Some liana species are prevalent in almost all high altitudinal gibbon habitats in Yunnan, and they might be the key to the gibbon's ability to survive there.

Black gibbons are both frugivorous and folivorous, but concentrating foraging efforts on ripe fleshy fruit resources when they are available. All the preferred food plants are patchily distributed across the home range except species from parasitic family Loranthaceae. During periods of fruit scarcity, the focal group switched to a highly folivorous diet and adjusted its activity budget accordingly. Deciduous trees and parasitic shrubs can be very important food for the gibbons because of their more stable availability in disturbed habitats. Their activity pattern and time budget is not so different from other small gibbon species.

The focal group home range was a long irregular shape with long edges covering 54 ha. Seasonal variations in habitat use were linked to relative differences in fruit resource abundance. Range use concentrated around local abundance of fleshy fruit resources. The gibbons can use both good forest and the scrub habitats adjacent to the forest. The study demonstrates that the black gibbons are similar to other small gibbons in activity pattern and ranging use, but in some features they behave like siamang (e.g. in being folivorous and with small day range area and short journey length). In general, black gibbons are a typical gibbon species, except for their possible polygynous mating system.

Two system models were developed to predict group size. The predictions of the models suggested that the group size in gibbons are both time constrained and resource constrained. The two models predict opposite trends: the time constraint model predicted that the gibbons can survive well in low rainfall habitats, but the resource constraint model predicted that gibbons survive better in high rainfall. These contrasting patterns limit gibbons to certain kinds of habitats that predict the actual distribution of gibbons quite successfully. The models suggested that polygyny occurs because group size can be larger in some habitats (such as those occupied by black gibbons).

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CHAPTER 1. INTRODUCTION

In Ancient China, the mysterious "YUAN" (Ape) — "猿" (the name of gibbon or apes in Chinese), attracted many, many people's eye. For over 2000 years, gibbon has been the subjects of numerous essays, poems and paintings in China (van Gulik, 1967; Liu, 1980; Gao *et al*,. 1981). People noted that gibbons are similar to ourselves, displaying acrobatics, and singing songs, but it is not an easy job to watch them ... *As songs of gibbons from both side (of Yangtzi River) are still echoing in my ear, ship has crossed thousands and thousands mountains...* (Li Bai, Tang Dynasty, 701-762 A.D.). Human's curiosity towards gibbons has a long history (Chen, 1995).

Terms "hylobatids" and "lesser ape" are used to label collectively all the animals of the family Hylobatidae, sometimes "gibbon" of similar use, but it usually refer to all taxa except "siamang". Siamang is specifically used for *H. syndactylus*. Various species of gibbons are now scattered in the remaining forest patches of South and Southeast Asia. In contrast to great apes, hylobatids are the most primitive hominoids, with small bodies and little sexual dimorphism. They inhabit primary tropical and subtropical forests.

As part of the ongoing global biodiversity crisis, all gibbon species are threatened, to various degrees, and some populations are probably on the verge of extinction. Habitat forest destruction is the most significant factor contributing to the decline of all gibbon species. The ancient Chinese literature shows that gibbons may have been distributed as far north as the Yangtze River (ca. 31°N, 110°E) as recently as 1000 years ago. Today, however, Chinese gibbons are confined to Yunnan and Hainan provinces, and are on the verge of extinction (Tan, 1985; Ma and Wang, 1988; Lan, 1995; Zhang, 1992; Zhang, 1995). Urgent research and conservation action are needed to change the worsening trends. The persistence of many of the gibbon species will largely rely on active conservation measures (Mittermeier, 1987).

1.1. Gibbons ---Basic Information

1.1.1. Distribution, Classification and Field Studies

The history of detailed gibbon taxonomy is not long: George de Buffon described the first gibbon in 1776 (Preuschoft and Creel, 1984). Subsequently, most species were described in the 1800s (*e.g. H. concolor*, Harlan, 1826). Living species are distributed from Assam and Bangladesh in the west, Yunnan and Hainan in north, then Burma, Laos, Vietnam, Cambodia, Thailand, Malaysia and Indonesia in the middle and south.

Generally, it is accepted that all gibbon species are placed in a single genus, *Hylobates* (Groves, 1972) (**Table 1-1**). Four subgenera based on karyotypes are recognised: *Nomascus* (2n=52), *Symphalangus* (2n=50), *Hylobates* (2n=44) and *Bunopithecus* (2n=38) (Prouty *et al.*, 1983; Marshall and Sugardjito, 1986). *Symphalangus* and *Bunopithecus* each has a single species, namely *H. syndactylus* (the 'siamang') and *H. hoolock*, respectively. However, no gibbon classification systems is universally accepted at present. The main controversies involve the question on how many species there are within the so-called 'lar-groups' and the *Nomascus* group or "crested group".

The subgenus *Hylobates* contains *klossii* and the so-called lar-group. The number of species within the lar group is highly controversial, but usually 5 species are recognized: *H. lar, pileatus, molock, agilis* and *mueleri* since 1970s (Chivers, 1977; Marshell *et al.*, 1984).

Table 1-1. Classification of genus *Hylobates* (Hylobatidae, Primates, Mammalia).

Subgenus	Species	Common Name
Symphalangus		
	H. syndactylus	Siamang
Bunopithecus		
	H. hoolock	Hoolock gibbon
Nomascus		
	H. concolor	Black gibbon
	H. leucogenys	White-cheeked gibbon
	H. gabriellae	Red-cheeked gibbon
Hylobates		
	H. klossii	Kloss gibbon
	H. lar	White-handed gibbon
	H. pileatus	Pileated gibbon
	H. moloch	Silvery gibbon
	H. muelleri	Muller's gibbon
	H. agilis	Agile gibbon

Table 1-2. Classification of subgenus *Nomascus* (Hylobatidae).

Species	Subspecie
Hylobates leucogenys	
Hylobates gabriellae	*H. g. gabriellae*
	H. g. siki
Hylobates concolor	*H. c. concolor*
	H. c. nasutus
	H. c. hainanus
	H. c. jingdongensis
	H. c. furvogaster
	H. c. lu

Black gibbons belong to the subgenus *Nomascus* (**Table 1-2**). The taxonomy of *Nomascus* has received substantial attention in the past two decades. It has been indicated that the subgenus has two species, resulting from the splitting of *H. leucogenys* from *H. concolor* (Dao, 1983; Ma and Wang, 1986; Ma *et al.*, 1988). Groves and Wang (1990) not only support this division, but also append one more full species, *H. gabriellae*, or the red-cheeked gibbon. Some also suggested that *H. c. hainanus* should be split from *concolor* to hold a full species status (Su *et al.*, 1995).

The first gibbon field study was carried out in northern Thailand by Carpenter (1940) on *H. lar* in 1937 (Carpenter, 1967). Since then, all gibbon species have been studied, more or less, in the field, except some members of the *Nomascus* group (*e.g. H. gabriellae*). *H. lar* has become the best studied gibbon species, and is currently still under intensive field observation (Brockelman *et al.*, 1998; Palombit, 1995). Review of most field work from the 1940s to 1980s are available in Chivers (1984) and Leighton (1987). Since then, some more work has been carried out, mainly on lar, siamang, hoolock, concolor and leucogenys (black gibbon: Liu *et al.*, 1989; Lan, 1989; Sheeran, 1993, 1995; Jiang *et al.*, 1994a, b, c; 1997; 1999; Chen, 1995; White-cheeked gibbon: Hu *et al.*, 1989, 1990; hoolock gibbon: Islam and Ferroz, 1992; Ashan, 1994; lar: Brockelman *et al.*, 1998; Reichard, 1995; 1998; Reichard and Sommer, 1994; lar and siamang: Grether *et al.*, 1992; Palombit *et al.*, 1993; 1994; 1995; 1997).

1.1.2. Evolution

Hylobatids are the oldest offshoot inside Hominoidea (apes and humans) and the most primitive hominoids (Haimoff *et al.*, 1982; Fleagle, 1984). Within hylobatids, based on anatomical, behavioural, karyological and molecular studies (*e.g.* Cronin *et al.*, 1984; Haimoff *et al.*, 1982; Preuschoft and Creel, 1984; Prouty *et al.*, 1983), the siamang, *Nomascus* spp., the hoolock gibbon, the kloss gibbon and the lar groups are the five highly distinctive groups of extant lesser apes. The essential evolutionary relationship of the five groups are generally agreed: the *Nomascus* spp., the siamang and the hoolock gibbon are the oldest offshoots, the lar group members the latest and the kloss gibbon in the middle (Chivers, 1977; Creel and Preuschoft, 1976; Haimoff *et al.*, 1984).

Except for *H. syndactylus* (siamang, about 12 kg) which is sympatric with two small gibbons (*lar* and *agilis:* both about 5 kg), all other gibbon species are allopatric, being mainly separated by waters. Only small sympatric areas are found between other species, such as between *lar* and *pileatus* in Khao Yai, Thailand (Brockelman, 1978; Marshall and Sugardjito, 1986), *concolor* and *leucogenys* in northern Vietnam and south Yunnan (Dao, 1983; Ma and Wang, 1986) and possibly *lar* and *concolor* in southwest Yunnan (Haimoff *et al.*, 1987b; Lan, 1995a). Limited natural hybridization is known to occur within lar groups (Marshall *et al.*, 1984).

1.2. Gibbon Ecology and Behaviour

The pioneering gibbon study of Carpenter (1940) established the fundamental characteristics of gibbon behaviour: frugivory, territoriality and monogamy. Most subsequent studies have confirmed these findings. Some small differences existed between species, especially in siamang and black gibbons (Siamang: Chivers, 1974; Haimoff *et al.*, 1986; Black gibbon: Chen, 1995; Liu *et al.*, 1989). As those little known species (*e.g. leucogenys, gabriellae* and *concolor*) are under study, along with the new findings in the recent long term studies (Brockelman *et al.*, 1998; Palombit, 1994; 1995; 1996; Reichard, 1995), new revisions may be necessary for the understanding of the gibbon behaviour, especially social behaviour.

1.2.1. Ecology

Gibbons are completely arboreal. They are typically found in monsoon, evergreen rain forests (Chivers, 1977). They occasionally inhabit more seasonal, mixed evergreen and deciduous or semi-deciduous forests (Sheeran, 1993), but they never inhabit completely deciduous forests (Tenaza, 1975).

Within these preferred forests, gibbons live where tree diversity is usually high. It is suggested that the preference for diverse forests ensures a consistent supply of sugar-rich fruit throughout the year (Gittins, 1982). Species diversity makes dietary shifts possible during lean times, as at least one tree species will be fruiting at any given time. A folivorous strategy might be adopted by gibbons when fruits are few in poor habitats.

Gibbons have been observed feeding on leaves, shoots, stems, flowers, bird eggs, and invertebrates, but they are particularly frugivorous relying on fruits like figs (*Ficus*) (Chivers, 1984, 1986; Gittins, 1982; Kappeler, 1984; Leighton, 1987; Srikosamatara, 1984). In general fruit comprises about 60% and leaves 30% of the diet for most of the smaller gibbons, and figs comprise over 20% of the dietary intake for most gibbon species. Most species rely on foods (such as figs) that can be rapidly ingested with little preparation time (Gittins, 1982). The larger siamangs (Chivers, 1974), and some black gibbon populations (Lan *et al.*, 1993), are more folivorous, while *klossii* gibbons apparently obtain protein primarily from insects instead of young leaves (Whitten, 1984). Hoolock gibbons, which are similar to the size of concolor gibbons (larger than other gibbons but smaller than siamang), show a highly frugivorous diet (90%) when and where fruits are available (Islam and Feeroz, 1992), or a highly folivorous diet (50%) where fruits are scarce (Mukherjee, 1986).

At two study sites in West Malaysia, siamang diets average slightly more leaves than fruit, but reach 60% fruit in some months (Chivers, 1974; MacKinnon and MacKinnon, 1977). In the fig-rich forest at Ketambe, Sumatra, siamangs appear to be more consistently frugivorous (Palombit, 1997). Simang and lar groups with overlapping ranges have diets more similar to each other than to neighbouring groups of the same species, but these similarities belie important differences in feeding ecology (Gittins and Raemaekers, 1980; MacKinnon and MacKinnon, 1977). Simangs eat leaves at a faster rate and eat more leaves that are mature or nearly mature. They visit fewer food patches (*i.e.*, trees or lianas) each day, have longer feeding bouts, travel less far between patches, and appear to rely more on larger-sized fruit patches (Gittins and Raemaekers, 1980).

Gibbons are not fastidious feeders, wasting a great deal of food as it falls from their mouths. They compete with squirrels, birds, and other primates in their exploitation of fig fruits and leaves. In general, gibbons eat near ripe or fully ripe figs, while other non-human primates eat unripe ones (Lambert, 1990). Gibbons also ingest their largest daily dose of figs at dawn, possibly to avoid competing with monkeys who tend to eat later in the day (Raemaekers, 1980). As gibbons might lack plant detoxification abilities, they usually do not exploit mature leaves although these are eaten by other sympatric monkeys (langurs and macaques)(Gittins, 1982). Gibbons can take advantage of large conspicuous fruit sources, but mainly rely more on small inconspicuous fruit sources for a constant food supply, and for avoiding competition with other species (Gittins, 1982). Some research has shown that the hylobatids are important dispersers of fruit tree seeds because the process of digestion does not prevent subsequent germination (Lambert, 1990, Whitington and Treesucon, 1992).

The food resources the gibbons forage on are usually small and patchily distributed, which other primates do not utilise effectively (Leighton, 1987). A gibbon group carefully monitors the fruiting status of all trees in an area which is proposed to be large enough to meet the group's dietary requirements, but small enough to be searched frequently and protected by the group (Gittins, 1982). The group gains an intimate knowledge of each tree within its territory (Chen, 1995; personal observation).

1.2.2. Ranging, Activity and Territoriality

Gibbons have fixed home ranges that average about 34 hectares, with exclusive portions (territories) averaging 75% of this area. Siamang home ranges are smaller than those of sympatric lar groups, but similar in size to those of many other gibbon species. Presumably, the siamang's more folivorous diet permits smaller territories than expected for its larger body size. Home ranges of hoolock (Mukherjee, 1986) and black gibbons (Chen, 1995; Jiang *et al.*, 1994b; 1999; Lan, 1989; Liu *et al.*, 1989) show a marked variation, and are possibly the largest of all gibbons. Some studies also suggested that black gibbons are possibly with weak or no territoriality (Liu et al., 1984, Jiang et al., 1994c). Within species, home range size and gibbon densities can vary as much as fivefold between study sites (*e.g.*, *klossii* and *lar*).

Gibbons are active from 8 to 10 hours a day on average. Activity usually starts at dawn and stops well before sunset. Adult males and offspring become active sooner and often stay active later than adult females. Singing and the most intense feeding occurs in the morning, but compared to most other primates, gibbons show little change in activity over the day. Gibbons spend most of their day foraging in the main canopy (c.a. 20 to 35 meters high in primary forest). If they exist, emergent trees are primarily used for rest, sleep, and singing. Little time is spent in the lower canopy, and this mostly to visit small food trees (Gittins and Raemaekers, 1980).

Most gibbon species travel more or less 1000 meters a day (Leighton, 1987), although some (*muelleri*, *pileatus*, *syndactylus*) travel a little less, about 800 to 900 meters. *Agilis* often take only 10 to 15 minutes to cross from one side of their territory to the other (Gittins, 1980). Gibbons use their ranges unevenly, but tend to visit most sectors every few days. *Lar* and *agilis* normally take 2 to 3 days to cover their ranges completely, while *syndactylus* take 6 days (Gittins and Raemaekers, 1980). Food is an important determinant of range use (Ellefson, 1974). There is no strong evidence for patrolling behaviour in gibbons, and boundary disputes normally do not affect ranging patterns in *agilis* (Gittins, 1980). However, simulated intrusions using play-backs of gibbon duets have elicited immediate, temporary monitoring of the territory by siamangs (Chivers and MacKinnon, 1977) and, less explicitly, by *muelleri* (Mitani, 1985b).

Territoriality in gibbons is considered to have evolved in relation to resource protection or mate protection (Brockelman and Srikosamatara, 1984; Chivers, 1977; Dunbar, 1988). Morning vocalisations of gibbons are probably the most conspicuous territorial advertisement behaviour (Marshall and Marshall, 1976; Raemaekers and Raemaekers, 1985).

During calling, group members may engage in such territorial behaviours as branch shaking, rapid brachiation, and rigid posturing (Marshall and Marshall, 1976). These activities are typically directed toward the territory of neighbouring groups, but they are not necessarily precipitated by a physical encounter with a neighboring group or unfamiliar gibbons (Gittins, 1982). The reaction of neighbours to a group's territorial song depends on the degree to which the singing family has trespassed on the territory boundary (Mitani, 1984, 1985a). These complicated vocal and visual activities are consistent with being a general territorial advertisement (Mitani, 1985a). As such, they function to indicate the family's existence and willingness to protect resources within the territory. Additionally, because in most species the morning song bout involves a complex interaction between adult male and female, it is hypothesised that dueting reinforces the pair bond (Deputte, 1982; Cowlishaw, 1992).

1.2.3. Family Structure and Mating System

Most gibbon species normally live in small monogamous groups (Leighton, 1987), with debated possible exception of *H. concolor* (Haimoff *et al.*, 1987a; Jiang *et al.*, 1994a,b; 1999; Lan, 1989, 1990a; Lan et al., 1990; Lan and Sheeran, 1995; Liu *et al.*, 1989; Sheeran, 1993). Traditionally, gibbons are believed to live in nuclear family groups, and characteristics of this model include that gibbons mate for life, mating is generally exclusive between mates, immature animals in the groups are the descendants of the mated pair, and new groups are ordinarily formed by newly dispersed individuals (Brockelman and Srikosamatara, 1984; Gittins and Raemaekers, 1980). However, there are some exceptions (Ashan, 1995; Haimoff *et al.*, 1987a; Quiatt, 1987), and some strongly exceptional cases have recently been found in some long term field studies (Brockelman, *et al.*, 1998; Palombit, 1994; 1995; 1996; Reichard, 1995). These studies found out that new pair-bonds are frequently created through mate replacement by individuals either from within the same group or other groups. Out-group mating also existed.

The nuclear family group of gibbons averages four individuals: one adult male, one adult female, and their offspring (Chivers, 1984). The typical group consists of two breeding adults, a juvenile offspring, and an infant. Gestation lasts approximately 8 months, and the interbirth interval is 2 to 2.5 years (Edwards and Todd, 1991), but also possible practically longer up to 3-4 years in some groups or species (Geissmann, 1993; Palombit, 1995). Sexual maturity is attained at six to eight years (Tilson, 1981; but see Geissmann, 1991).

When a young gibbon reaches sexual maturity, it peripheralizes from the group's main activities. Peripheralization may entail an active repulsion of the young animal from the family by the same sexed parent (Carpenter, 1964; Chivers, 1974; Chivers and Raemaeker, 1980; Edwards and Todd, 1991; Tilson, 1981), but sometimes the young gibbon is increasingly excluded from family activities. These peripheralized animals may be observed near the core of the family, but they interact infrequently with the family. Studies indicate that peripheralization can be a passive, gradual occurrence, taking years to complete (Chivers *et al.*, 1975) or it can be the result of a more dramatic, physical interaction (Aldrich-Blake and Chivers, 1973).

The final goal of peripheralization appears to be the dispersal of the sexually mature offspring. Males may be the sex which initiate territory establishment. Females from neighbouring families are attracted to the lone male by its vocal activity. The young male travels across the territories of several nearby families in its search for a mate. Young females may also range across neighbouring territories during this time (Sheeran, 1993).

Females do not always leave the natal family upon reaching sexual maturity. They may be tolerated and possibly even incorporated in the natal family if territory resources permit (Bleisch and Chen, 1991; Srikosamatara and Brockelman, 1987), while males apparently attempt to establish their own territory. Unfortunately, the process of the female's peripheralization and leaving is less well known than that of the males.

Because of the spatio-temporal distribution of gibbon families there is a high potential for philopatry which may be adaptive in these circumstances for the following reasons. First, parents may provide aid in establishing new territories. Second by remaining near its parents, a young male may inherit his natal territory, which is probably superior to any territory the younger animal could obtain on its own. Third, the dispersing individual may benefit from predator avoidance and food procurement by remaining close to familiar areas. Cowlishaw (1992) estimated that the transient individuals suffer a high mortality (about 50%).

Because gibbons are philopatric, most populations are probably inbred. The chromosomal evidence indicates that gibbons have probably been inbred at least since the evolution of the existing species (Marks, 1987). Habitat fragmentation in recent years has increased the tendency for inbreeding by isolated populations in small patches of forest.

A young male attracts potential mates by his solo long calls. The distance a gibbon call travels depend on many factors: vegetation type, distribution and density; climate, size and sex of calling individuals and the location of the callers (Deputte, 1982; Haimoff, 1985, Haimoff *et al.*, 1987a; Kappeler, 1984a).

When a newly bonded male and female have established their territory, it might take several years for the pair and the territory boundary to become stable. Both sexes contribute to the maintenance of the territory and the pair bond, either by vocalizations or boundary disputes (Brockelman, 1984; Gittins, 1984b, Marshall and Marshall, 1976). However, Cowlishaw (1992) showed that male calls are not territory-related, as prevalently believed, but for attracting females.

Because male reproductive fitness is often better served through polygyny (Davies, 1989; Dunbar, 1988), gibbon monogamy were described as 'female enforced' (*e.g.* Leighton, 1987; Mitani, 1987). This view is supported by the way in which mated animals respond to 'strangers' of both sexes. A mated female will repulse strangers of both sexes, while a mated male tends to respond more aggressively to unmated males (Mitani, 1987), which suggests that he would tolerate additional adult females. In the few cases in which more than one adult females are observed in a family, the 'surplus' individual has been a female (but not necessarily the male's mate and possibly his daughter or step-daughter: *pileatus*, Srikosamatara and Brockelman, 1987; *concolor*, Bleisch and Chen, 1991; Liu *et al.*, 1989). Hybrid females have also been observed living with established pairs, probably because the mated female did not recognise the hybrid female's song and therefore did not attempt to evict her from the territory (Brockelman and Srikosomatara, 1984). This condition does not necessarily reflect a breakdown of monogamy, but may be due to the retention of a subadult female when suitable mates are unavailable or when dispersal options are limited (Bleisch and Chen, 1991). Thus, some primatologists suggest that female distribution across territories and interfemale aggression are the overriding factors which sustain monogamy in gibbons (Mitani, 1987; Leighton, 1987; Jiang *et al.*, 1994b, 1999).

It is proposed that a nuclear family group of gibbons appears to maximise the utilisation of small, patchily distributed food resources (Gittins, 1982; MacKinnon and MacKinnon, 1984). A small group of gibbons can better exploit these resources than can a large monkey troop. Their dietary strategy of frugivory, and reliance on small patches of inconspicuous fruit, have been hypothesised to be the ultimate factor determining a monogamous mating system for gibbons (Brockelman and Srikosomatara, 1984; Wrangham, 1987); however, infanticide risk (also less plausibly predation risk) has been proposed as an alternative explanation for monogamy in this unique primate group (van Schaik and Dunbar, 1990).

1.3. Aims and Thesis Outline

1.3.1. Aims

Compared to other gibbon species, little is known about the black gibbons. Our understanding of this species is too superficial to make any comparison with other gibbons successful. So one aim of this study is to increase our knowledge of this species. The black gibbons are the most northerly distributed species, and with the highest altitude habitats. As we know, these kinds of habitats are usually low quality, so they are likely to be under some ecological stress. In the present study I aim to detail the behavioural ecology of this poorly known gibbon species, *Hylobates concolor*, through the understanding their unique habitat, time budget, feeding and ranging; then I will try to explain how the black gibbons cope with energetic and nutritional stress to survive in marginal habitats.

1.3.2. Thesis Outline

Chapter two provides details concerning the study site and outlines the broad field methodologies incorporated within this study. Chapter three then examines group dynamics: distribution, group size and dynamics of those groups which I observed and studied since the 1980s, in order to give a background understanding for the data presented in other chapters and the questions I am going to ask. The possibility that polygyny or multi-female groups may be a regular feature of the black gibbon mating system will be a question of particular interest.

Chapter 4 is concerned with the habitat quality. Since the habitat of black gibbons is different from other gibbons, I present a detailed study of its climate and forest and comparison with other studies and species. Chapter five is concerned with the activity budget of the focal group. The overall, monthly and diurnal activity budgets are outlined, and age-sex class difference are presented.

In chapter six, I present feeding behaviour in relation to food availability, food types and food preference, and discuss how the gibbons deal with the shortage period of food. In Chapter 7, I examine ranging behaviour and habitat use by the focal community in relation to temporal changes in the distribution of the dominant fruit resources. The size and shape of the focal group home range is interpreted in the light of these results.

In Chapter 8, I compare the difference within the hylobatids and ask whether black gibbons are unique among the hylobatids? Then in Chapter 9 I will present and test socio-ecological models to evaluate the ecological tolerance of gibbons. I will discuss their unique features, especially like one-female or multi-female grouping, nuclear family size and frugivory.

CHAPTER 2. STUDY SITES AND METHODS

In this chapter, I will present outline information about study sites (**2.1-2.3**) and basic methodology (**2.4-2.8**). As for the black gibbon, details of the main research groups, methods for ageing and sexing, and group composition will be presented in **Chapter 3**.

I. Study Sites

2.1. General Geographical Context--- Yunnan Province

Yunnan Province (**Figure 2-1**) is located in the Southwest China. To the west and south, it is bordered by Burma (Myanmar), Laos and Vietnam. From northwest to east lie Tibet, Sichuan and Guangxi Provinces. Yunnan is a medium sized province of China with an area of 380,000 km^2, and a population about 39 million in 1997. Kunming is the capital city of Yunnan Province.

Yunnan has diverse habitats resulting from the immense elevation range from the highest point of 6740 meters above sea level (Mt. Meilixueshan) to the lowest spot at 76 meters above sea level (at the intersection of the Red River and the Chinese- Vietnamese border). Therefore, climatic conditions also vary dramatically from the low and hot south to the high and cold north, especially towards the northwest. The altitude is the main factor determining the climatic condition (Liu *et al.*, 1989, Wu *et al.*, 1987).

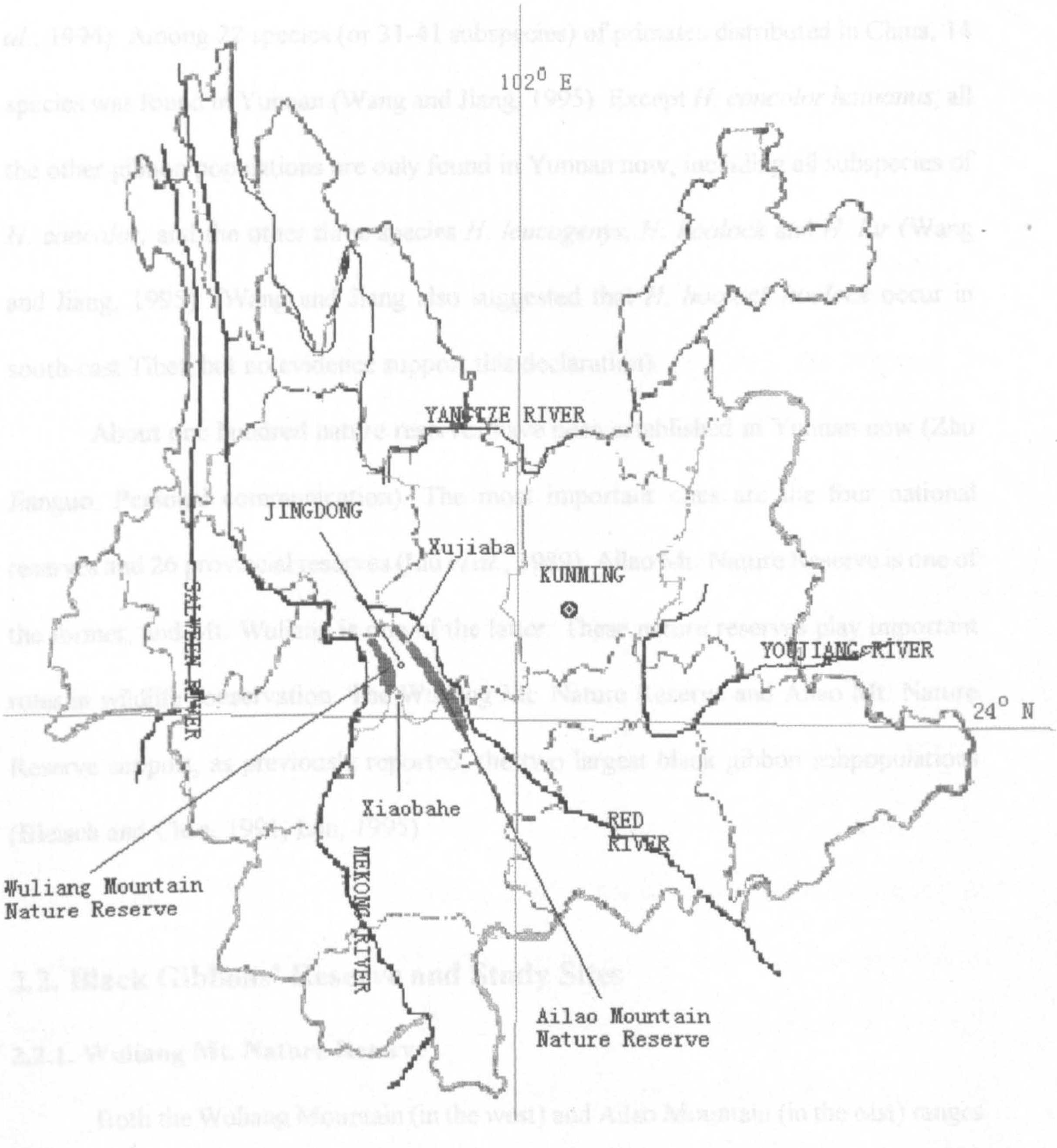


Figure 2-1. Map of Yunnan Province, showing two study sites and the nearby nature reserves and other relative geographic features.

Yunnan has a high rating in biodiversity conservation. For example, 250 mammals and 766 species of birds are found in this province (Wang *et al.*, 1994; Yang *et al.*, 1994). Among 22 species (or 31-41 subspecies) of primates distributed in China, 14 species was found in Yunnan (Wang and Jiang, 1995). Except *H. concolor hainanus*, all the other gibbon populations are only found in Yunnan now, including all subspecies of *H. concolor*, and the other three species *H. leucogenys, H. hoolock* and *H. lar* (Wang and Jiang, 1995). (Wang and Jiang also suggested that *H. hoolock hoolock* occur in south-east Tibet, but no evidence support this declaration).

About one hundred nature reserves have been established in Yunnan now (Zhu Jianguo, Personal communication). The most important ones are the four national reserves and 26 provincial reserves (Liu *et al.*, 1989). Ailao Mt. Nature Reserve is one of the former, and Mt. Wuliang is one of the latter. These nature reserves play important roles in wildlife conservation. The Wuliang Mt. Nature Reserve and Ailao Mt. Nature Reserve support, as previously reported, the two largest black gibbon subpopulations (Bleisch and Chen, 1991, Lan, 1995).

2.2. Black Gibbons' Reserve and Study Sites

2.2.1. Wuliang Mt. Nature Reserve

Both the Wuliang Mountain (in the west) and Ailao Mountain (in the east) ranges run from north to south in south-central Yunnan (Liu *et al.*, 1989). Those parts of the mountain land where forest was still dense when nature reserve designation was declared in 1980s are defined as nature reserve. Wuliang Mt. Nature Reserve is located on the north-central part of Wuliang mountain range. Administratively, the reserve lies entirely within Jingdong county, although the mountain range into several counties in the north and south. My intensive study sites, Xiaobahe, is not in the county of Jingdong, but just bordered with it. So strictly speaking, contrary to the report of other scholars (Bleisch and Chen, 1990, 1991; Haimoff *et al.*, 1986, 1987a,b; Jiang *et al.*, 1994a, b, c; 1999; Sheeran, 1993; 1995; Zhang *et al.*, 1995), Xiaobahe is not in the nature reserve.

In 1950s, following the suggestions of local (Yunnan) scholars to the governors, a much smaller part of the present reserve within the Wuliang mountain was nominated as a nature reserve (Anonymous, 1960). But the real nature reserve delineation and management did not become established until 1987. The designation was approved by Provincial government and later by central government (Liu *et al.*, 1989). From 1950s to 1980s, the forest and wildlife in and around the mountains suffered serious destruction. Presently, only areas above 2000 m asl have primary forest and are designated as nature reserves (Haimoff *et al.*, 1987b; Lan, 1989). The major part of the reserve is within the range of 2400 -2800 m altitude.

However, the reserve is still under intense human pressure from its proximity to villages, cultivation land and vehicle roads. Most parts of the forest of the reserves are local traditional reservoirs for firewood, honey, herbal medicine and other forest products. Due to the doubling of the human population, along with bad management of economic activity (*i.e.*, commercial logging with low effectiveness in resource utilisation), the nature reserve faced a high pressure. Virtually all suitable land below the reserve borders has now been cultivated (Bleisch and Chen, 1990; Haimoff *et al.*, 1989; Lan, 1995).

On the west site of the reserve is the valley of the Mekong River at 900-1000 m above sea level, and on the east is the upper part of Black River at 1100 m above sea level. The Wuliang Mountain range is rather large (north to south 250km by 50-70 km wide east to west), but the total nature reserve is only 233.95 km^2 and limited to the central-north part, with a very elongated shape of about 50 km long and about 6 km wide at the widest part of the reserve.

2.2.2. Ailao Mountain

Ailao Mt. Nature Reserve is located on the Ailao Mountain range. Administratively, the reserve is located in the central to north part of the range, within the range of 5 counties, namely, Chuxiong, Shuangbai, Xingping, Zhengyuan, and Jingdong. Ailao Mt. Nature Reserve is of almost half as big again as Wuliang Mts. Nature Reserve (Chen, 1995; Liu *et al.*, 1989).

It has a similar history to Wuliang Mt. Nature Reserve, but was later promoted as a national reserve. As with the whole Wuliang area, this reserve is under intense human pressure around its immediate borders. Virtually all suitable land below the reserve borders has been cultivated. The top of this mountain suffers more serious human disturbance, because the terrain at the top is much more gentle than that of Mt. Wuliang. The reserve lies from about 1800m above sea level to nearly 3200 meter. However, the major part of the reserve is within the range of 2400- 2700m.

The west boundary of the mountain range is formed by the Babian River at 1000 m altitude (upper part of Black River). On the east side, lies the Shiyang River (upper part of the Red River) at 900 m above sea level. The Ailao Mountain range is rather large, too (north to south 300 km long by 70- 90 km wide east-west). Of this large area, the total area of the reserve is 350 km^2, also with an elongated shape of about 100 km long and about 6 km wide at the widest part of the reserve. Compared to Wuliang nature reserve, owing to its bigger area, Ailao nature reserve has been promoted to be the National-level and Man and Biosphere (MAB) nature reserve.

The other nature reserves containing black gibbons are of similar characteristics. Although some of them are not of elongated shape, almost all reserves are located at the top of the mountains. These include reserves of Daxueshan, Fenshuiling, Huangliangshan, Daweishan, etc. Between these reserves, the land is used heavily as cities, villages development and cultivated land.

2.2.3. Xiaobahe

Xiaobahe is located in the southern tip of (but just outside) Wuliangshan Nature Reserve (**Figure 2-1**), although it lies at the centre of the whole mountain range. The map co-ordinate is 24°20'N, 100°47'E. This site have been used by previous studies (named as 'Bayenza' by Haimoff *et al.*, 1986, 1987; and Xiabahe by Lan, 1989, 1993, 1995; Jiang *et al.*, 1994a, b, c, 1997; 1999; Sheeran, 1993, 1995; and only referenced as Wuliang mountain by Bleisch and Chen, 1990, 1991) (**Figure 2-2**). My main study group, Group B, is living in this area. Must other groups observed are mainly located at this district, too, ore neighbour to this district, details see **Chapter 3**.

"Xiaobahe" means "a small river runs over a little basin". The basin is very small and corresponds exactly to the riverbed. The basin has been used by local people occasionally about 50 years ago, when they planted potatoes and opium poppy there during certain seasons of the year. No cultivation occurred after 1950s. In the past, possibly a long time ago, parts of the basin and slopes, mostly on the west bank of the stream, were cut and set on fire to make grazing grassland. The local people continue to set fire to parts of it once a year or so, for the purposes of grazing goats, sheep, oxen and buffalo. So now, only remnants of forest patches remain. The forest is now in the shape of a spider with a body and long legs.

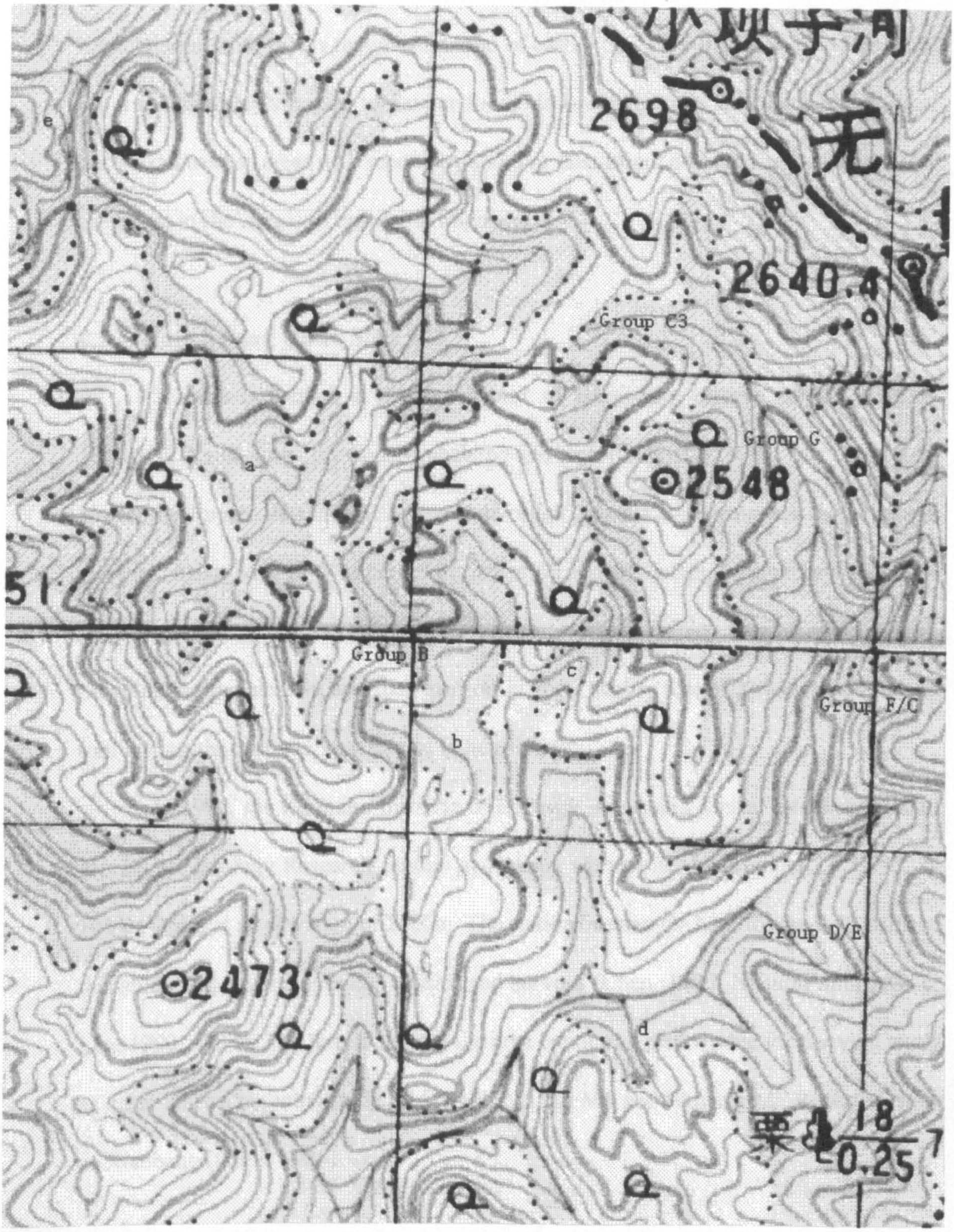


Figure 2-2. Xiaobahe---the study site, show the forest patches and landscape and group location.

In the past two decades, the local people have adopted another way to use the mountainous land, that is they plant a kind of cash crop, 'Hua Jiao' (*Zanthoxylon* spp), the fruits of which are used to flavour foods. In order to make land for planting, local people cut trees in areas with secondary shrub or (less often) primary forest. So presently the forest in the area is to becoming fragmented.

2.2.4. Xujiaba and Other Sites

Xujiaba is located in the north part of the nature reserve, about 24°32'N, 101°01'E. Xujiaba was previously inhabited and a plot of land of 60 ha was completely cleared by former inhabitants. A reservoir called Xujiaba Reservoir was built there in 1958 and enlarged in 1988 as part of the irrigation system for Jingdong county. When the reservoir is full at the end of the rainy season, it has a surface area of about 1 km^2. Surrounding the clearing and the reservoir is good quality forest. Xujiaba is on a main trail linking the east and west slopes (Chen, 1995).

In 1980, the Kunming Institute of Ecology, Academia Sinica, established Ailao Mt. Forest Ecology Research Station at Xujiaba with its headquarters at 24°32'40" N 101°01'35"E at an elevation of 2400m. The station became the base for the field work of this study and several previous studies and surveys (Chen, 1995; Haimoff *et al.*, 1986; Lan, 1993; 1995). The terrain around the area is not as unfavourable for carrying study as other known potential study areas in both Ailao Mt. and Wuliang Mt. Reserves, such as Xiaobahe (Chen, 1995).

2.3. Climate, Seasonality, Vegetation and its Zonation

Most parts of Yunnan are mainly influenced by the monsoon of the Indian Ocean, which results in two distinct seasons of approximately equal duration. In general, the wet season extends from late May into mid or late October, and during this time approximately 80 to 90% of the precipitation falls. The dry season begins in late October and lasts through to mid or late May.

In general, average annual rainfall for most black gibbon habitat is between 1700 and 2000 mm (Lan 1989). The annual average temperature in the region is 11° C. But in those upper sub-mountain areas (usually above 2000 m asl) or on the peaks of the mountains, temperatures can drop to freezing and snow is not impossible in winter (Chen, 1995). The climate in the reserves (usually located at the upper part of mountain ridges) was quite different from that experienced in the surrounding valleys.

For most nature reserves, forest type varies along the elevation gradient. Below 1800 m, there are only pine forests left, in general. Between 1800 to 2100m, both pine forest and evergreen broad leaf forest can be found. From 2100 meters to 2600 meters lies the so called 'middle mountain humid broad -leaf evergreen forest.' Above 2600 m, stunted mountain forest occurs, featuring short trees and shrubs. For the specific climatic and forest characters of the two main study sites (Xiaobahe and Xujiaba), the data will be presented in detail in **Chapter 4**.

2.4. Sympatric Primates and Other Competitive Frugivorous Species

In the area where black gibbon are distributed, there are 5 other primate species including Phayrei's langur (*Thachipethecus phayreii*), Stump-tailed macaques (*M. arctoides*), Rhesus macaques (*M. mullata*), and possibly pig-tailed macaques (*M.*

nemestrina) and slow loris (*Nicticebus coucang*). The altitudinal distribution of the primates represented in Jindong county are shown in **Table 2-1** (He *et al.*, 1992; Wang *et al.*, 1994).

Table 2-1. The primate species and their habitat altitudinal distribution in Jingdong county and adjacent area.

Species	Habitat altitude
Hylobates concolor	1800-2800
Trychipithecus phayreii	1800-2900
Macaca mulatta	900-2900
Macaca arctoides	1500-2900
Macaca nemestrina	900-2000
Nicticebus coucang	900-1800?

In Mt. Wuliang and Mt. Ailao, I found 3 of these species (*i.e.*, langur, stump-tailed macaques, rhesus macaques) in a few areas. One pigtailed macaque was checked after it was caught by local villagers, outside the forest area, near the cultivated land and village.

There are many other mammal species in the area. Presently the competitor frugivorous species are mainly mammals and birds. The other mammals which possibly compete for fruits with gibbons, are some Rodentia species, tree shrews, and Carnivora species such as bear (*Selenarctos thibetanus thibetanus*) (Wang *et al.*, 1994).

II. General Methods

2.5. Climates: Sites and Data Collection

The ecological research station at Xujiaba maintains a small weather station. There the climate data have been continuously collected since the 1980s. Daily climatic records were taken after the procedures of the Chinese national standards for small scale climatic stations. At Xiaobahe, I have established a simple weather station which is similar to that at Xujiaba, but with less recording items.

We used several ways to collect the climatic data. The temperature and relative humidity were taken by a mechanical auto-recorder (Shanghai Weather Equipment Factory). The thermometers were also used to measure both the maximum and minimum temperatures outside and inside the forest (30 meter from the edge of the forest). Evaporation and precipitation were measured in a forest opening using a bowl of 20 cm diameter. At our camp site, we put all instruments mentioned above except for evaporation and precipitation measures on a table under a tree trunk 1.2 meters above the ground, at the edge of the forest. To avoid direct sunshine and rain, thermometers were in shade throughout the day and could be read accurately to the nearest degree. The rain gauge is in an opening, away from any tree and our camp house, to maintain disturbance-free.

The data analysed for Xujiaba come from the Ecological Station. According to their general procedure, the temperature both of the dry and wet thermometers were taken at 8 am, 2pm and 8pm. Daily evaporation was measured at 8pm, and precipitation was recorded three times a day. Dates on which condensation and snow fall occurred were recorded. At Xiaobahe, the data were sampled in general in late afternoon, usually 7pm, which let the data represent the past 24 hours.

Other data used here are from the local weather stations when I visited them during my field trips or from publications. In general most weather stations, are established in the valleys, usually because these are heavily populated and cultivated areas (such as county towns and cities). Most nature reserves are usually located in remote areas: quite a lot at the top of the mountains. So data from those publicly available sources are not liable if we consider the real habitat of gibbons seriously in its unique altitude bands.

The general climatic conditions were also recorded everyday. The foggy, windy, snowing, and frost days were recorded too. Specific wind condition and general weather condition were usually sampled when we were observing or listening for the gibbons, especially at 7am, 1pm and 7pm hours because these times evenly span those hours of daylight when gibbons are active (Sheeran, 1993). We score the wind on 5-point scales: no wind, breeze, small wind, strong wind, and super strong wind.

In summary, for the analysis here, data are available from Xujiaba (black gibbon), Xiaobahe (black gibbon), Gaoligongshan (hoolock gibbon), Nanguanhe (lar gibbon).

2.6. Vegetation Sampling

2.6.1. Plots Distribution and Size

I established 18 plots in the area at Xiaobahe in 1994, each of them 20x20 m^2. In order to compare the plant food resources availability within home ranges between polygynous and monogamous groups, I added some more plots and use some other methods to collect the vegetation data. At first, I planned to measure 3 1-hectare plots within the home range of Group B, as was done by Chen (1995) in his research group at Xujiaba. I found it is impossible to do this kind of big plot because of the terrain, so I established 20 20x50 m^2 plots within the home range of Group B, and added 7 plots of 20 x 20 meters in the ranging area of group G, where I had not placed any vegetation survey in 1994.

We also placed some 20x20 m^2 plots in other sites where the habitat showed it might be different from Xiaobahe (usually judged by altitude) to allow for comparison between sites. Kainnanhe river is not far away from Xiaobahe, but there the gibbon group ranged at lower altitudes, so we measured 9 plots nearby at between 1670 to 1950m in elevation. The group KNH ranged about 400 m lower than the groups at Xiaobahe.

In 1998, we used another way to compare the habitats of gibbons between Xiaobahe and Xujiaba, which concentrated on the woody liana species and their abundance. We established 200m transect lines randomly within the census area and selected five points along the line, every 50 meters. At each of those points, we divided the area around the point into four quadrants and measured the individual tree nearest to the point in each quadrant. Based on those points, we also checked all woody liana species and their individual numbers, measuring the diameter at the point where they finally leave the ground to the canopy (with diameter larger than 2.5 cm), within the 10 meter circle centred on the point. Along the transect line, we also recorded the canopy cover at 10 m intervals on a present/absent basis.

2.6.2. Canopy Measurement

We measured the canopy of each tree by estimating the crown cover area by the longest diameter and shortest diameter. At first we also measured the height of the crowns. But since this was not a very accurate estimation, I finally discarded the measurement data, but used the basal area cover to measure the productivity, as other studies have done (Barrett, 1995; Wallace, 1998).

However, we did measure tree height, and the highest point of the canopy, of the points along the middle and two side lateral lines of sampling plots (20x50 m^2). We used these data to calculate the canopy height.

2.6.3. Diameter Measurement and Species Identification

In the plots of 20x50 m^2 or 20x20 m^2, all trees with diameter at breast height (DBH) of 10 cm or over were measured and identified, and all woody climbers stretching into the canopy were identified in the field. Only woody climbers with ground-level diameters larger than 5 cm were sampled. Plant identification was done with the help of Mr. S. C. Li and Dr. H. Peng, both of them are experts on local plants. Mr. Li was from the ecological station at Xujiaba, and had helped Chen (1995), Zhang *et al.* (1995) and other scholars who study plants or animals in the area (Xie *et al.*, 1997). Dr. H. Peng is from the Kunming Institute of Botany, whose PhD is about the plants of Mt. Wuliang, and he has experience of working in Mt. Wuliang for 6 years (Peng, 1997).

2.7. Phenology and Food Availability Assessment

Around my base, along the Xiaobahe river, more than 100 tree and liana species have been identified and monitored for phenological condition. More than two healthy individuals of each species were selected and marked, other individuals were also checked from time to time. At least 2 individuals were checked for phenology, since some species have asynchronous production cycles.

From January 1997, observation and recording of each species was carried out 3 times separated by 10 days within each month (in general, on the 5th, 15th and 25th of each month). Routine phenological observation was usually done by my assistants, Li Shouchang at Xujiaba and Mr. Zhang Xinjun at Xiaobahe.

For each observation, individual trees were registered as one of the following categories: new leaf (including leaf shoots), flower-bud, flower, young-fruit, ripe fruit, dropping fruit (naturally), defoliating (naturally), old-leaf or no-leaf. A species was very often recorded as falling in several categories in a single observation. For example, evergreen species were entered as 'old-leaf' for every observation, while they could also be flowering, fruiting, etc., at the same time. Another example is that some deciduous species could become completely defoliated while fruits remained, so they were recorded as 'no leaf' and 'ripe fruits'.

During analysis for food availability, only fruits, young leaves, and flowers are of high value as food for black gibbons, so all categories recorded above were lumped into four categories: fruits (ripe or unripe), old leaf, young leaves (also including buds and shoots), flowers.

From October 1997 to September 1998, within or near the home range of group B, five individuals each of 24 species which were found to have been eaten frequently or with high food value potentials in previous studies were monitored to assess the abundance of food parts. The categories recorded include the existence of the part (such as fruits) and the abundance (in 5 categories, 0; 1: 1-25%; 2: 26-50%; 3: 51-75%; 4: 76-100%). The list of the species can be found in Appendix. These data are used to assess food availability and its seasonal variation.

2.8. Behavioural Observation

Point scan sampling (Altmann, 1974; Dunbar, 1976; Martin and Bateson, 1986) at 10 minute intervals was used to gather data on activity budgets, diet and social and ranging behaviour. Scans lasted for 1 minute and data were collected on as many animals as possible during that interval. The total number of animals included in any one scan depended on group members' activities; some easily observed active behaviours, such as feeding and moving might be over-represented. The various behaviours that were recognised during point scan sampling are detailed in **Table 2-2**.

Conspicuous behaviours such as agonistic calling and looking at observer were recorded on an all occurrence basis (Altmann, 1974; Martin and Bateson, 1986). Loud vocalisations and alarm calls, given by following groups and/or nearby groups were also monitored, and the time, location, duration, context, and any responses were noted.

The location of the group was continuously recorded with reference to the trail-stream-slope system. Since I observed the group outside the forest, it is possible to use the water system to check the altitude where the group was. When the group members changed their location for more than 10 meters, it would be recorded down on the map on the recording note books, and later converted to standard ranging maps. In addition, if possible, locations were recorded for scan samples every 10 minutes. During extended bouts of travel, additional locations and associated times were recorded opportunistically when the group crossed a recognisable point on the map. The movements of the focal group were also mapped continuously on a standard map of the study plot.

Table 2-2. Summary of data variables recorded for each point scan sample.

Variable	*Definition*
Time	Time at beginning of ten minute interval
Climate	Cloud, precipitation, and wind (0, no wind; 1, breeze; 2, light wind; 3, strong wind; 4, super strong wind)
Location and habitat type	Location with reference to trail-stream system and corresponding part
Group spread	Two dimensions like a cross.
Group activity	Dominant activity of visible subgroup members
Observed group size	Continuously recorded when it is possible to having more than one in the sight view
Identity	Age/sex class of subject, where possible identified.
Activity Rest	Sit or lie inactively, also clinging if it last more than 5 seconds.
Feed	When the animal eat anything, such as picking, sending to mouth, chewing
Move	Brachiating, bridge, clamber, climb, descend, leap, slide, swing, or walk on the truck.
Singing	Call and when the gibbons emits sounds, usually morning songs.
Others	All other activities excepts those listed above, including allogroom, autogroom, charge, defecate, dispute, embrace, Nurse, play, scan, urinate
Distance of observation	Estimated distance from observer
Forest edge or non-edge	Point near the forest edge, like within 10 meters at least in one site, not primary evergreen forest left.
	Point locates at more than 10 meters to the either side of the edge of the forest.
Food species and part	Feeding tree species and food part (*e.g.* ripe fruit, unripe fruit, flower, bud leaf)

CHAPTER 3. DISTRIBUTION AND SOCIAL GROUP STATUS

3.1. Introduction

Distribution is important information for effective conservation action. The Yunnan is the main distribution area of black gibbons. The earliest record of black gibbons might be from the Anderson's field collection in Yunnan (Allen, 1938). However, no data about history and trends of extinction and disappearance of gibbons are available, since no well-planned systematic surveys have been carried out in the past. The documentation of the species' distribution and the changing trends in the gibbon population have only begun to attract attention since1980s. During the 1980s, based on increased broad survey, field works, specimen checking and studying, some papers have been published which relate to the species' distribution and habitat (Fodden *et al.*, 1987; Lan, 1995; Li and Lin, 1983; Ma and Wang, 1986; 1988, Yang et al., 1987). Virtually all black gibbon populations and habitat have now been subjected to disturbance from human activities. It is necessary to review the present distribution of this species to give a rough background for the understanding of its geographic characteristics and later for determining what conservation action is necessary.

Several recent studies have focused on black gibbons, *Hylobates concolor* (**Table 3-1**). Some studies suggest that this species may be polygynous or multi-female groups (Delacour, 1933; Haimoff *et al*, 1986;1987, Jiang *et al.*, 1994a, b; 1999; Lan and Sheeran, 1995; Liu *et al.*, 1989). It is reasonable to believe that the behaviour of this species may differ markedly from that of other gibbons because of their specific habitat characteristics (Bleisch and Chen, 1991; Haimoff *et al*., 1986).

H. concolor in the wild have proven to be difficult to observe, because they are very wary of humans, probably because of intense hunting pressure. Rugged terrain and the lack of habituation of any groups have further hampered research efforts on the understanding of the behaviour and ecology of black gibbons. At present, the black gibbon is in danger of extinction throughout its range, primarily because its restrictive habitat requirements make it especially vulnerable to deforestation, and its behaviour and low reproductive rate make it vulnerable to over-hunting (Bleisch and Chen, 1990). In the past decade, I have tried to survey, study and monitor this endangered species in the wild. Here I present observational results and synthesise the results from other researches (mainly from Mts. Wuliang), in order to shed some light on the grouping pattern of this unique gibbon species.

3.2. Survey and Research Review

In 1985, Haimoff *et al* carried out first ecological observations on black gibbons in Wuliang and Ailao Mountains in Yunnan, China. They reported 7 groups heard or seen, with 6 groups having more than two adult females, so they suggested that black gibbons are polygynous (Haimoff *et al*., 1986). One and a half year later (1987), another short study was conducted at almost the same sites (Bleisch and Chen, 1990, 1991). Bleisch and Chen later reported that, in 3 groups, 2 female singers were heard. However, they could not confirm whether any of these group were polygynous. Since the same year (1987), I have carried out a much longer field study, including a broad survey and intensive observations in south-west Yunnan. The intensive site is called Xiaobahe, near the study site of Haimoff *et al.* (1986, 1987a) (Bayenza) and Bleisch and Chen (1990, 1991). My results suggested that this species was still monogamous although I could not absolutely reject the possibility of polygyny, based on the survey data (Lan, 1989; Lan *et al.*, 1990).

From 1990 to 1991, Sheeran, Ma, and Jiang further studied the behaviour and ecology of the Xiaobahe black gibbons in Mts. Wuliang and Mts. Ailao (Jiang *et al.*, 1994a, b; 1999; Sheeran, 1993). Jiang *et al* (1994a, b; 1999) reported that, among 5 groups they observed, one group (C3) was two-female group and possibly polygynous. But one of their research team member, Sheeran suggested that the extra adult female was 'one female developing the mature pelage' in the group (Sheeran, 1993). Furthermore, Chen (1995) carried out a long-term study at Xujiaba in Mts. Ailao which provided some useful ecological data for this species, although he reported that the groups were all monogamous. However, some specific results suggested that polygynous groups do exist in this species. In addition to the record by Jiang *et al.* (1994a, b, 1999), Lan and Sheeran (1995) mentioned that one single female group changed into a two-female group with two adult females after 1993. As for outside Yunnan, multi-female groups polygyny have been reported in Hainan since early 1980s (Liu *et al.*, 1984, Liu *et al*, 1987, 1989; Xu *et al*, 1983; Xu *et al*, 1984). All these findings arouse a lot of new discussion, but most people would probably agree that polygyny may be ephemeral.

Although a final conclusion is difficult to draw, these studies nonetheless provide more and more data supporting the possibility of polygynous mating system and multi-female social grouping in this species.

3.3. Survey Site and Method

I have conducted a broad survey and research on black gibbons in Yunnan Province, starting in 1987, totaling about 30 months field work. The survey covered several mountainous areas of both nature reserve and non-nature reserve, including Wuliang, Ailao, Banma, Yongde Daxueshan and Lingcang Daxueshan (mountains), and Nangunhe (river) (Lan, 1989; 1995a). All these sites are located in Southwest Yunnan, between 22°13'-25°N, 98°54-101°05'E. Our main efforts were on a site called Xiaobahe, where most other researchers have also carried out their studies (Lan 1995a). Some of my previous study results have been summarised and published elsewhere (Lan 1989, 1993, 1995a, b, Lan *et al.*, 1990a,b). The most recent studies, on which the following analysis is based, are listed in **Table 3-1**. The aging and sexing of black gibbons are similar to other studies (Lan, 1989; Liu et al., 1989; Sheeran, 1993).

Table 3-1. Field studies on black gibbons since 1985.

Time	Researchers	Area	Publications
1985	E.Haimoff N.Chen	Mt. Wuliang Mt Ailao	Haimoff *et al.* (1986 1987a b)
1987	W.Bleisch N.Chen	Mt. Wuliang Mt. Ailao	Bleisch and Chen (1990 1991)
1987	D.Yang	Mt. Bangma	Yang and Xu (1990)
1990-1994	X.L Jiang S.L Ma	Mt. Wuliang and Mt. Ailao	Jiang *et al.* (1994-1999)
1990-1994	L.Sheeran	Mt. Wuliang and Mt. Ailao	Sheeran (1990-1995)
1991-1993	N.Chen	Mt. Ailao	Chen (1995)
1993	Zhang, Quan, Yang, Sheeran	Mt. Wuliang and Mt. Ailao	Zhang *et al* (1995)
1987-1998	Lan D.Y.	Whole Yunnan, mainly Mts. Wuliang and Ailao	Lan (1989-1995)

3.4. Distribution of Black Gibbons in Yunnan Province

Based on my survey and other scholars' work, I concluded that there are about

250 groups of black gibbons distributed between 3 subspecies (**Table 3-2**). The highest estimation of all black gibbons in Yunnan does not exceed 600 groups since all other sites are of small area, worse forest conservation status and more heavily hunted compared to Wuliang Mountain and Ailao Mountain. None of them can have more gibbons than Wuliang Mountain (*H. c. jingdongensis*) and Ailao Mountain (*H. c. concolor*) Nature Reserves.

Table 3-2. The estimation of black gibbon population in Yunnan*.

Researchers	*Hylobates c. concolor*	*H.c. jingdongensis*	*H.c. furvogaster*	*H. concolor* (Total)
Tan, B.J.(1985)	4(g)[a]	6-7(g)		
Haimoff, *et al.* (1986)		25-250(g)		
Yang, D.H. *et al.* (1985, 1987)	133-190(i)[b]	195-231(i)	319-329(i)	
Ma and Wang (1988)	40-60 (i)	300 (i)		
Ma, S. L. *et al.* (1993)	600-700(i)	250-300(i)	80-100(i)	
Zhang, Y.Z. *et al* (1995)		81(g)		
Lan (1989)	>5(g)	66-144(g)	>1(g)	
Lan (1995)	75-150(g)	66-100(g)	30(g)	206-600(g)
Present estimation	75-150(g)	66-100(g)		

* a, (g), means counting in group number; b, (i), means counting in individual number.

A lot of censuses, surveys and studies have been carried out in the Mts. Wuliang area since 1985. In 1960s, the scientists from Kunming Institute of Zoology had collected specimens there for study. At the time, the population was still large. The numbers of gibbons recorded in the sites in my surveys from 1987 are listed in **Table 3-3,** and some other sites with accurate records of black gibbons are listed in **Table 3-4**.

Table 3-3. Sites where I have recorded black gibbons during survey*.

Sites	Longitude (E)	Latitude (N)	Altitude (x100m)	No. of group Heard	Status	Survey time
Xiaobahe[1]	100°45-9’	24°19-22’	22-26	7	H	1987-98
Shangchanghe[1]	100°43-5’	24°18’	22-25	2-3	P	1988-98
Kainanhe[1]	100°49’	24°18-9’	18-19	1	H	1987-1998
Wuguiba[1]	100°40’	24°22-3’	22-24	1	P	1988
Xizhang[1]	100°36-38’	24°33-34’	20-26	1	P	1993
Wangjiachun[1]	100°34-5’	24°37	22-26	1-2	P	1988-97
Wenpo[1]	100°42-43’	24°27-9’	24-27	2	P	1988-98
Huangcaoling[1]	100°44-5’	24°22-3’	23-25	2	P	1988-1998
Xujiaba[2]	101°00-05’	24°22-34’	23-26	5-8	P	1988-1998
Jianxing[2,a]	101°37’	23°48’	23-24	2	H	1992
Pingzhang[2,b]	101°36-7’	23°52-3’	22-26	1	H	1992
Bangma[3]	99°47’	23°42-43’	23-24	1	H	1989

* P: protected; H: threatened by hunting and logging. 1=belongs to Wuliang Mountain range, 2=belong to Ailao Mountain range. 3 is Bangma Mountains. [a]The northeast area of Erqin Reservoir; [b]Xiaoliangshan or Pomiechang.

3.4. Xiaobahe: How Many Groups are There?

The number of groups at Xiaobahe is somewhat confused. Jiang *et al.* (1994a, b) reported there were 5 groups, and Sheeran (1993, 1995) 4 groups. My own observations gave an estimate of 5-6 groups, in the immediate area of Xiaobahe. [For the whole northern part of Zhengyuan county, and the adjacent eastern slope of Datuanshan in Jingdong county, there are about 16 groups or more, as reported in Lan (1995a, b)]. These areas are adjacent to the nature reserve, but are not included in the formal Wuliang Mountain Nature Reserve designation. Bleish and Chen (1991) only reported one group observed at Xiaobahe, although they heard more than 3 groups there and nearby (Bleisch and Chen, 1990). Based on the map they provided, this group occupied half to 3/4 of the total Xiaobahe area.

Table 3-4. The others sites at which the black gibbons have been found and recorded in past several decades.

Shibazhai in Mts. Ailao, 24°15'N, 101°20'E, by Jiang *et al.*, (1994a): work carried out June to July 1990.

Xiangjinghe, in Mt. Ailao, 24°00' N, 101°25'E. Jiang *et al.* (1994a) work conducted during March to May, 1991.

Huangcaoba in Jinggu county. No coordiantes available (possibly near 101°3'E, 23°29'N). The black gibbons in this area were confirmed by a field survey carried out in 1997 (Ma Shilai. and Yang Xiaojun, personal communication). That is the first time black gibbons have been recorded in Jinggu county. The population is small and belongs to the subspecies *H. c. jindongensis.* The site is about 100 km south to the previously reported sites.

Wayao. A district of Baoshan County. In 1960, some gibbon specimens collected there by Quan G.Q. (Fooden *et al.*, 1987, Quan Guoqiang, pers. comm.).

Wokandashan. Recorded by Ma and Wang (1986). It is reported that a few groups still existed there in 1995-6 (Wang Zhisheng, personal communication).

One reason why the number of groups varied so much is that the delineation of the area called Xiaobahe is unclear. Xiabahe (in the original) is a 4.7 km long brook, a tributary of the headwater of River Weiyuanjiang, which eventually flows into the River Mekong. Among local people, Xiaobahe mainly refers to the upper part of the brook. The habitat of group B, although crossed by a small stream, which flows into the Xiabahe river is not included in Xiaobahe.

If only the watershed is included, the Xiabahe area is about 5.4 km^2. Since gibbon groups also range outside the watershed of the Xiaobahe, the general delineation for the area is usually extended to include an area larger than 5.4 km^2. Sheeran *et al.* (1998, manuscript) gave an area estimation of 11 km^2 for Xiaobahe, with 7.7 km^2 of the area covered by forest (70%). No map and no detailed delineation are provided in her paper.

Taking account of the terrain, I estimate the area defined by a square of the four grid lines of 100°46'E, 100°48'E, 24°19'N, 24°21'N, with the location referred to as Xiaobahe by the local people in the center (China PLA, 1964), has a total area about 12.63 km^2. If one side of the rectangle, 100°48'E, is replace by a side at 100°49'E, then the area is 18.51 km^2. Based on a sample of 450 small quadrats, about 65.8 % of the area is covered by forest. So the forest area is 12.18km^2. They are connected by either corridors of primary or secondary forest or the shrub vegetation on the peaks of the mountains.

Within this area, there are four groups (B, F, G, C3), and possibly 2 to 3 other groups (such as group H: Lan, 1989; 1990a). Based on an estimate of 6 to 7 groups, we can calculate a group density of 0.324-0.378 groups per km^2, or 0.49 -0.57 per km^2 of forest area. Based on these density data, the total number of groups within the Wuliang Mountain Nature Reserve (233.95 km^2) is estimated as 82 groups (ranged 76 to 88).

If we limited Xiaobahe to the area where groups B, F, G, D, E and C where recorded by singing or direct observation, then there are possibly 5 groups (B, F, G, C3, and one unclear). The black gibbon groups overlap with each other heavily. In the main area of the Xiaobahe, Bleisch and Chen (1991) observed one group. They suggested that my groups (D, E, F and G) and Sheeran's (1993) groups (CA, CB, C3) are possibly all the same group. Both Jiang *et al* (1994a, b) and Sheeran (1993) suggested that there were at least 4 groups (not including B) across the whole area. Group codes for each researchers are listed in **Table 3-6**.

This inconsistency is possibly caused by the difficulty of differentiating groups, and the difficulties of the observation. If we cannot differentiate them by singing or observation, groups may easily be confused. Group E and group D in those tables are possibly the same group, identical to CA of Sheeran (1993) and GB1 of Jiang *et al.* (1994a, b). Only one group was easily recognised by most researchers, that is B (=GA or C1). From 1997 to 1998, I could only recognise 2 or 3 groups separately at the site.

Table 3-5. The group codes, site codes and successful direct observation and counting in different year*.

Year	Xiaobahe (WLS)	Xujiaba (ALS)	Group code in other study sites
1987	B,H,L,K		
1988	B,D,E,K	X11, X12, X13, X14	WP1(Wenpo, WLS) WJC1(Wangjiachun, WLS)
1989	B,D,E,F		MS1(Mengsha, Bangmashan)
1992			PZ1(Pingzhang, Xingping co., ALS)
1993	B		
1994	B		
1997	B,F,G,K	X15	
1998	B,F,G,K		SCH1(Shangchanghe, WLS) KNH1(Kainanghe, WLS)

*Note: Those studied sites and period without direct group counting and observation I have not included here. WLS=Mt. Wuliang range, ALS=Mt. Ailao range.

Table 3-6. The group codes used in each study.

Group Code in This Study	Range size (ha)	Jiang et al	Sheeran	Bleisch and Chen
B	50-60	GA	C1	
D and/or E F	Ca. 200	GB1 GB2	CA	W1
G	Ca. 150	GB2 GC1 GC2	CB C3	W1

Haimoff *et al.* (1986) calculated that the group density is about 0.88 groups/km^2 at Xiaobahe (above 2400 m sea level) and nearby, and 0.18-0.3 at Xujiaba. Although I do not have exact gibbon density data at Xujiaba and other sites, gibbon group density and biomass seems to be higher at Xiaobahe than at Xujiaba, as most study shows (Haimoff *et al.*, 1986; Lan, 1989, 1995a; Ma, 1994; Zhang *et al.*, 1995).

3.5. Group Composition and Dynamics

Since 1987, I have recorded 15 groups at different times over the 11 years (**Table 3-5**). Except for three lone individuals, all other groups were of more than 2 individuals. Most of them were single-female group (with only one adult female in the groups). Two groups were two-female groups. One of the two groups, had been in single-female group when first sighted, then changed to being two-female group about 6 years later. The other group which I tried to observed in my field study in the 1980s, but found in my recent field study (1997-98), was two-female group. Another group was single-female recently but may have been two-female group in 1990-91 (Jiang *et al.*,1994a, b, 1999).

Group B which I have monitored and studied intensively since 1987, has two adult females with the typical yellow coloration of sexual maturity, and each of them carried an infant. I observed this group 3 times during 1993 and 1994. From the end of 1996, I continued to observe this group, and found it to be still two-female group, each female having infants of similar size and age. Group composition was stable from February 1997 to October 1998, and it looks like it really is polygynous (**Table 3-7**).

During 1998, we found another group of two adult females, group SCH, without any infants. The group had 3 to 4 black individuals. This group was also stable in composition between April and July 1998. We tried to check it again later, but could not count it properly. This group was reported to consist of 5 individuals in 1995 with only one adult female (**Table 3-8**) (Jiang and Wang, 1997).

Table 3-7. Change in size and composition of group B*.

Time	Size	Composition	Comments
1987	4	1AF 1AM 1B-C 1 JUV	
1988	4?	1AF 1AM 1 JUV 1 INF?	Only 3 were counted
1989	4	1AF 1AM 1JUV 1 INF	
1990	4	1AF 1AM 1B-C 1 JUV	Based on Jiang *et al.*(1994a), Sheeran (1993)
1993	6	2Afs 1AM 1JUV 2INFs	
1994	6	2Afs 1AM 1JUV 2INFs	
1997(1)	8	2AF 1AM 2B-Cs 1JUV 2 INFs	Before February 1997
1997(2)	7	2AFs 1AM 1B-C 1JUV 2INFs	After February 1997
1998	7	2AFs 1AM 1B-C 1JUV 2SINFs	At least until September

*AF, adult female; AM, adult male; B-C, black colour unsexing individuals, almost of adult size or a little bit small (possibly sub-adult); JUV, individuals of juvenile size; INF, infants or individuals of small size depending on the adult females.

Table 3-8. The size and composition of group SCH.

Year	Size	Compositions	Sources and comments
1995	5	1AF 1AM, ? ? ?	Jiang and Wang (1997)
1998	5-6	2AFs 1AM 2-3 B-Cs	This study

At Xiaobahe, another group (C3 of Jiang *et al.*, 1994a, b) was observed with two adult females and two juveniles of similar age (Jiang *et al.*, 1994a, b) . However, Sheeran (1993) suggested that one of the females was on its way to developing adult female pelage (**Table 3-9**). It seems that studies carried out at the same site during the same time period have reported different numbers of groups (*e.g.* Jiang *et al.*, 1994a, b; Sheeran *et al.*, 1998, manuscript). Their studies reported group size and compositions that varied over time, or groups that seemed to overlap heavily. Some groups seem to be missing completely (Jiang *et al.*, 1994a, b; Sheeran *et al.*, 1998, manuscript).

Table 3-9. The size and composition of group C3 or G at Xiaobahe*.

Year	Size	Composition	Sources
1990	6	2AFs 3B-Cs 1JUV	Sheeran (1993) Jiang *et al.* (1994)
1993[a]	?		No data available
1997	4	1AF 1AM 1B-C 1JUV	This study
1998	4	1AF 1AM 1B-C 1JUV	This study

* a. This group was reported absent since 1993 by Sheeran (1998, manuscript).

One group (G) was reported absent since 1993 by Sheeran *et al.*(1998, manuscript). However, based on my long-term monitoring, there still were groups ranging in the area in 1993-1994 and 1997-1998. Her results might be biased owing to her short study period. However, the group numbers and their range overlap remains confused.

The other groups observed with clear changes are listed in **Table 3-10** to **3-12**. Except for group K in **Table 3-12**, the other groups in the **Table 3-10** and **3-11** are a little bit confused. In the late 1980s, there were two groups (D and F) and possibly one solitary male ranging in an area of about 150 ha. The groups possibly existed in early 1990s (CA and CB by Sheeran, 1993), but later one group may have disappeared, and only F (or CB) is there, and now ranging into the area usually occupied by group D. The Group B also was observed ranging into group D's area in 1998 but not in late 1980s and early 1990s, since it is almost completely isolated from the area (Lan, 1989; Sheeran, 1993).

Table 3-10. The size and composition of group F or CB at Xiaobahe.

Year	Size	Composition	Sources
1989	5	1AF 1AM 2B-Cs 1INF	Lan (1989)
1990	5	1AF 1AM 2B-Cs 1JUV	Sheeran (1993)
1993	4	1AF 1AM 1B-C 1JUV	Sheeran (1998)
1997	4	1AF 1AM 1B-C 1JUV	This study
1998	4	1AF 1AM 1B-C 1JUV	This study

Table 3-11. The size and composition of group D/E/CA or F*.

Year	size	Composition	Sources
1988	4	1AF 1AM 1B-C 1JUV	Lan(1989)
1990	5-6	1AF 1AM 2-3B-Cs 1JUV	Sheeran (1993)
1993	At least more than 3		Sheeran (1998)
1997	At least more than 3		Sheeran (1998)
1998	4, group F	1 AF 1AM 1B-C 1JUV	This study

* This group might not be Group F during 1987 to 1990, since I observed that there were more than 2 groups singing within the whole area of the present range of Group F (1997-1998) or previous range of F and D (1988/1989).

Table 3-12. The size and composition of group K.

Year	Size	Composition	Sources
1988	3	1AF 1AM 1JUV	Lan (1989)
1997	5	1AF 1AM 1BC 1JUV1INF	This study
1998	5	1AF 1AM 2B-Cs 1INF	This study

3.6. Birth Season, Inter-birth Interval and Growth

3.6.1. Birth Season and Birth Intervals

The demographic data available on gibbons show no birth seasonality in most study areas, though most samples are too small to determine the existence of birth peaks. In some studies peaks appear unlikely or weak (*lar*: Captenter, 1940; *klossii*: Tenaza 1975; Tilson, 1981), but in more seasonal environments birth peaks may exist. All three hoolock births observed by Tilson (1979) at Hollongapar forest Reserve, Assam, India, occurred within a 2.5-month period (mid November to late January), which supports McCann's (1933) earlier observation of a possible hoolock winter birth peak. At Kuala Lompat, Malaysia, three of four births (one siamang and two lar births) occurred between November and January (Chivers and Raemaekers, 1980). Tilson (1979) and Chivers and Raemaekers (1980) speculate that birth peaks in gibbons may be timed to synchronize the commencement of weaning with periods of high fruit availability and may result from most conceptions occurring in seasons of high fruit abundance, but the data are insufficient to test this hypothesis.

Since October 1987, there have been at least 3, possibly 5, births in group B. The black gibbons may have a birth season during the late autumn and early winter, judging by the size of the infants observed.

In February and March 1989, we saw one black infant clinging to the female of group B: the infant would have been more than 12 months old since its fur color was black (Geissmann, 1991; Personnal observation, see below), but less than 18 months old because in October 1987 we recorded that the adult female was without infant (though possibly pregnant since it looked bigger than the male: Lan, 1989). In May and June 1988, we did not record infants in the group, possibly due to the difficulty of observing young infants because those less than one year old are similar in color to adult females. Thus, the infant would have been born after October 1987 and before April 1988, most likely between November and February 1988 judging by its size.

In June 1993. I found group B with two adult females, one with a black infant, one with a yellow one. The yellow infant was still yellow in September 1993, but changed into black in May 1994. Based on the age of color change and the pattern of infant-mother interaction, the black infant was estimated to have been born in late 1991, and the yellow one in late 1992. They therefore probably had different mothers.

In January 1997, we found that there were two adult females, both having yellowish infants clinging to them. Both the infants were very small. The two infants changed fur color from yellow into black, and gained some independence after November 1997. From these facts, we inferred that the two infants were probably born towards the end of 1996.

We estimated that birth intervals are between 4-5 years and 5-6 years for group B. For group K, there were possibly 2 births during 9 years since 1988, so the inter-birth intervals are about 4-5 years too.

3.6.2. Coloration of Infants

Two infants have been carried by the two adult females in the group B since January 1997. They were very small, and the fur was white-yellow; in the sunshine, the hair is almost white. These are the first few times we saw the two infants.

From the records in **Table 3-13**, we can conclude that infant gibbons develop black fur at the age of about 12 months old, and this change is completed by about 17-18 months.

Table 3-13. The fur colour of infants in group B during 1997-1998.

Dates	Fur colour description of infants
Jan to October, 1997	The infants are yellowish and white.
30 October, 1997	The infants were still yellow.
6 December, 1998	The infant is mainly yellow, but seem some parts are a little bit gray black.
10 January, 1998	One infant had began to change fur colour to black, but not completely. The other is still yellow.
13 February, 1998	Both infants are looks a little bit gray-black; at least one still looks of quite yellow.
21 February, 1998	One is almost black, especially much more black in the head. The arm is gray and black.
20 March, 1998	One infant is almost all black, but the other still has some yellow.
29 May, 1998	Both infants are black.
20 July, 1998	Both infants are wholly black now.

3.7. Discussion and Summary

The observations reported here indicate that black gibbon groups are pair-living for most time. Only a few groups were two-female groups and possibly polygynous. Interviews with the local people also reveals that two-female groups are not scarce, but occurs only at very low frequencies. Nonetheless, in this species, it seems that the occurrence of multi-female group is relatively higher than in other gibbon species (*i.e.*, hoolock gibbons in west Yunnan, personal observation; other gibbon species, Brockelman and Srikosomatara, 1984). In Hainan, Liu *et al.*(1987, 1989) reported one group having two adult females and two young of similar size and age (about 1 year different in age), which strongly suggested that this group was polygynous (**Table 3-14**).

Table 3-14. The sites and the groups reported to be polygynous in China*

Group Code [a] (year)	Site	Co-ordinates	No. of Adult females/off-springs [b]	Source [c]
B(1993-98)	Xiabahe, WLS	24°20'N, 100°47'E	2/2	This study
C3/G(1990-92)	Xiaobahe, WLS	24°20'N, 100°48'E	2/2	Jiang *et al.*, 1994a, b, 1999
SCH1/GS(1998)	Shangchanghe WLS	24°18'N, 100°44'E	2/?	This study [d]
ACXX(1978)	Xujiaba, ALS	24°33'N, 101°3'E	2/1-?	Zhou Yingjiu, Interview by Lan in 1988
WPXZ(1957-58)	Wenpu Xizou, WLS	24°27'N, 100°43'E	2/?	Ji Hongde, Interview by Lan in 1988
GD(1964)	Moudaohe, WLS	24°25'N,100° 39'E	2/2	Jiang *et al.*, 1994 a,b, 1999
AD(1971)[e]	Anding, WLS	24°43'N,100° 34'E	?/?[e]	Yang *et al*, 1985[e]
A, B (1985-8)	Bawangling, Hailan Is.	19°06'N, 109°18'E	2/2	Liu *et al.*, 1989

* WLS = Mts. Wuliang Range, ALS=Mts. Ailao Range. a. The code are based on original author if referred in Source, supplemented by code of this study if referred the same group. b. Numbers of adult female/offspings in the same age category. c, Data provider are listed here if it is my interview data. d. This group are not polygynous when Jiang and Wang studied on it (1995). e. This group are interview data by Yang *et al.*, and the provider is Wang Wenshan, the group code are given by me. The two yellow individuals are not sure were all adults or not.

What are the habitat characteristics of the habitat where the multi-female groups occur? In most sites, it seems that the habitat has suffered serious disturbance from human beings (**Chapter 2**). In general, only those gibbon groups which range in the edge of the forest can be easily observed and counted, and recorded. This is especially true of short surveys and studies, such as that by Carpenter (1940). Inside deep forest, it is difficult to find and observe gibbons, and the groups seen or observed are usually small in size and single female.

However, the habitats of the black gibbons are not the only ones to be disturbed by human activity; the habitat of other lesser apes has also suffered disturbance (*i.e.* lar groups in the northern Thailand: Carpenter, 1940). Why are black gibbons the only one to be multi-females or polygynous? This will be discussed further in the coming chapters through analysing its habitat, activity time budget, feeding and ranging.

CHAPTER 4. HABITAT—CLIMATE AND FOREST

4.1. Introduction

The habitat of black gibbons is unique among all gibbons. They have the most northerly distribution, at latitudes up to 25°N or more (One site recorded is 25°25'N), and the highest altitude, up to 2600 m above sea level (asl) or even more (Chen, 1995). The black gibbon could live, undoubtedly, in both low latitude and low altitude tropical areas. It does range in lowland forest in Vietnam and in Hainan, at least in the past (Liu *et al*., 1989). In Yunnan, it is generally distributed at higher altitudes, since most land in Yunnan province is above 1000 meters altitude. At present, almost all land under 2000 meters has been used by humans for anything else but for forestry. Cultivating and commercial forestry have expanded rapidly in the past 50 years and taken over most of the land suitable for wildlife including gibbons. However, no data about the detailed habitat study are available, except one by Chen (1995). His study was concentrated on climate and forest structure in just one site, without quantitative food availability analysis, and without comparisons, so cannot given an overview of all habitat of black gibbons.

Climatic data are a fundamental factor influencing animals' behaviour and ecology. Temperature and rainfall are related to seasonal changes which influence variation of food availability from month to month for gibbons (Gittins, 1980; Raemaekers, 1980). The weather conditions have been shown to influence the gibbon's singing (Kappeler, 1984; Leighton and Whitten, 1984), ranging (Gittins, 1982;

Raemaekers, 1980), and activity period (Chivers, Raemaekers, and Aldrich-Blake, 1975; Gittins, 1982; Raemaekers, 1980). Vegetation and food availability which was provided mainly by forest are important to hylobatids, and possibly the most important ecological factors in shaping their behaviour adaptation. In this chapter, I present the habitat characteristics of black gibbons by discussing the climates (**4.2 -4.4**) and vegetation and food availability (**4.5. -4.9**) which might influence the gibbon's life.

I. CLIMATE

4.2. Climate Patterns

4.2.1. General Overview

In general, climate is quite similar for most districts of Yunnan province. The prominent characters are the two distinctive seasons, dry and wet. Small differences exist among sites, due to altitude and the landscape, as well as latitudinal co-ordinates.

The climatic data of Xujiaba are very systematic since there are long-term records from the ecological station (Chen, 1995; Zhang, 1987). In the case of Wuliang Mountains, only anecdotal data are available before my study (Anonymous, 1960; Haimoff *et al.*, 1986; Sheeran, 1993). Instead, data for the valley area from the nearby county town meteorological station are assumed to be representative of the climatic conditions for the whole area. However, these data are really only representative of the situation in the low hot valley (mainly an agricultural area): the one meteorological station at Jingdong county town is located at the 1170 m altitude. Data obtained during earlier field studies (Haimoff *et al.*, 1986, 1987a; Sheeran, 1993) are available, but not year round, and can not give us a detailed description of the local climates.

As far as the main study sites are concerned, the weather is colder at Xujiaba than at Xiaobahe. Most other habitat areas lies usually to the south of these two sites, possibly experiencing warmer climates. Xiaobahe, for which most data are given here, cannot be treated as a typical habitat for black gibbons, since variation is obvious between sites. It might not be representative of the general conditions of gibbon habitat in the Wuliang Mts. Nature Reserve, too, since the Xiaobahe is at the southern tip of the reserve, and the diversified landscape makes the micro-climates very complicated.

Table 4-1. Temperature characteristics for different sites and/or years.

Sites	Xiaobahe (97-98)	Xujiaba (92-93)	Xujiaba (97)
Annual temperature (°C)	12.8	10.1	10.9
Average in hottest month (month)	16.5(Jun)	15.1 (Jun)	16.2(Aug)
Average in coldest month (month)	7.7 (Jan.)	3.6 (Jan.)	4.9(Jan)
No. of month with AT more than 10°C	10	6	6
Maximum temperature (Date)	25.5 (May)	21.9 (Jun)	25.2(Mar)
Minimum temperature (Date)	-3.3(Jan)	-5.1 (Jan)	-6.2(Jan)
Annual temperature range	28.8	27	31.4
Monthly highest range	25 (Mar)	17.7 (Mar)	28(Mar)
Monthly least range	12.6 (Jul)	7 (Jul)	11.3(Nov)
Frost days	37	44	22

For comparison, I also present basic climatic data of Xujiaba for the study period of 1997 and 1998. The annual data for Xiaobahe are presented from March 1997 to February 1998, unless otherwise specified. The climatic characteristics at the two main sites are shown in **Table 4-1** and **4-2.**

Table 4-2. The characteristics of precipitation for different sites and/or years*

Sites	Xiaobahe (1997)	Xujiaba(1992-3)	Xujiaba(97)
Total (mm)	2257.1	1530	2254.3
Evaporation (mm)	301.2	1383.8	
Wet season total[a]	1865.3	1326.4	1833.4
No. of month more than 100mm	5	6	7
Monthly highest total (month)	598.8(Jul)	338.2(Jul)	557.1(Jul)
Daily highest(date)	67.1(July)	66 (May)	139.6(Jun)
Rain days % of the wet season[1]	65	66	61

* a. based on the traditional figure such as from May to October. In 1997, the rainfall for May is less than 100 mm, but for April and November are more than 100 mm.

4.2.2. Xiaobahe

Temperature

Annual temperature was 12.8°C. The hottest month was June (mean=16.5°C) and the coldest month was January (mean=7.7°C). The months from March through December enjoy a monthly average temperature higher than 10°C, while the other 2 months sustained a monthly average lower than 10°C (**Figure 4-1**).

The highest temperature recorded was 25.5°C, occurring in May 1997, and the lowest temperature was -3.3°C, recorded in Jan. 1998 , which gives an annual range of 28.8°C. Monthly temperature range was greatest in March (25°C), smallest in July(12.6°C) . The largest daily range, 24.5°C, happened on March 7, 1997 , while the least, 1.5°C, was on July 4, 1997. There were 27 days in which the temperature dropped below freezing.

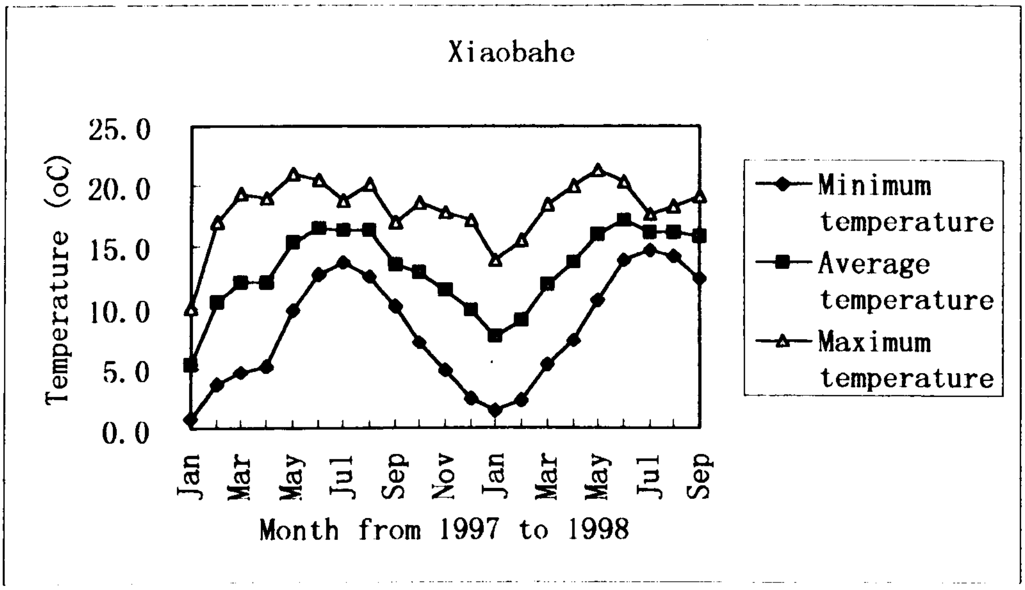


Figure 4-1. The temperature during study period at Xiaobahe, Mt. Wuliang, Yunnan.

Precipitation

Annual precipitation totalled 2257.1 mm, which greatly exceeded annual evaporation (301.18mm). Precipitation occurred unevenly throughout the year. For the whole year, monthly precipitation was higher than monthly evaporation, indicating a year-round humid environment.

Months with more than 100 mm precipitation, usually from May to October, are defined as wet season months (Chen, 1995). In 1997, the wet season came late, from June to October, lasting only 5 months. In 1998, the wet season came in May and lasted for 6 months. During the wet season a total precipitation of 1865.3 mm was recorded, which was 82.6 % of the annual total (**Figure 4-2**). The single day maximum rainfall was 67.1 mm, recorded on July 16, 1997. Highest monthly rainfall was received in July 1997, totalling 598.8 mm.

For a whole year (March 1997 to February 1998), there was a total of 172 rainy days, or 47.1% of the days. But just in the wet season, there was a total of 120 rain days, equivalent to 69.8% of all rain days in the year, or 65.2% of all days during the wet season. During the dry season, there were 52 rainy days, which was 28.4% of the dry season days. On the 120 rainy days in the wet season, the average daily precipitation was 16.04 mm (n=120, SD=15.35). In the dry season, the respective statistics are 6.7 mm (n=52, SD=7.62).

Rainfall was distributed rather evenly in the day time (0700-1900 hours) and in the night time (1900-0700 hours), but was a little bit more common in the night in the wet season. Snowfall was not recorded; only hail was recorded. Local people verified that there is snowfall in some winters, and snowfall was documented at Xujiaba by Chen (1995) (see below).

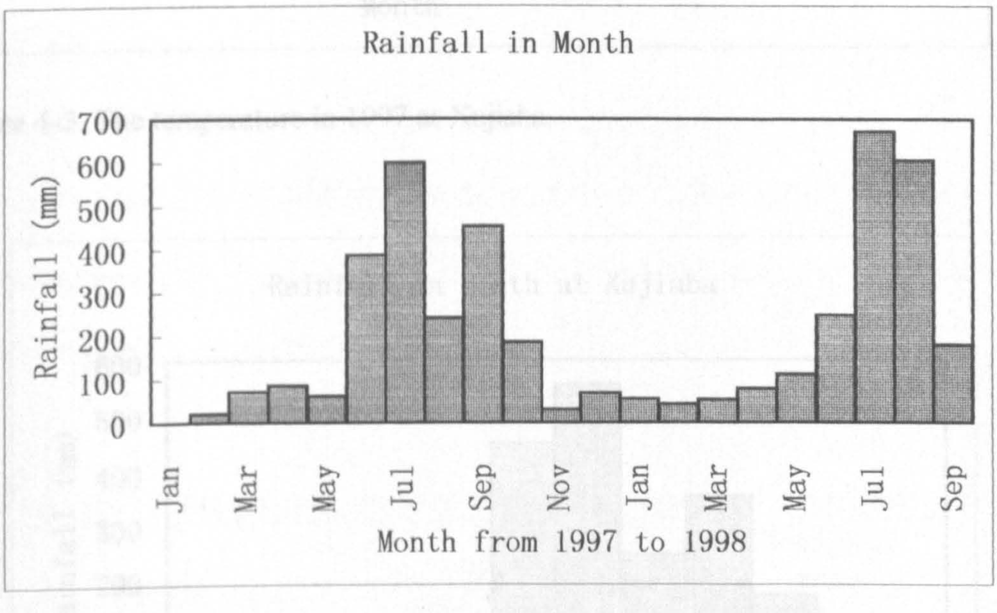


Figure 4-2. The rainfall distribution during study period at Xiaobahe.

4.2.3. Xujiaba

In the year 1997, the temperature and rainfall characteristics are summed with other sites in **Tables 4-1, 4-2** and **Figures 4-3** and **4-4**. The apparent difference is that it was colder at Xujiaba, compared to the Xiaobahe. Situation at Xujiaba reported by Chen

(1995), suggests that evaporation is higher than precipitation in some dry season months. We do not have evaporation data for Xujiaba for the study year 1997.

Compared to 1980s, the rainfall at Xujiaba in 1997 is higher, in 8 months. Some month receive 218mm more. These data show that there is yearly variation.

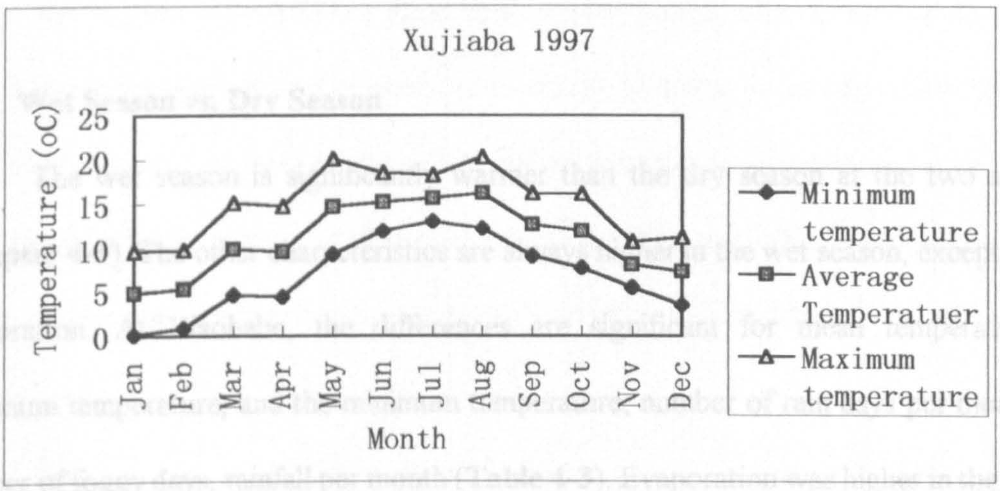


Figure 4-3. The temperature in 1997 at Xujiaba.

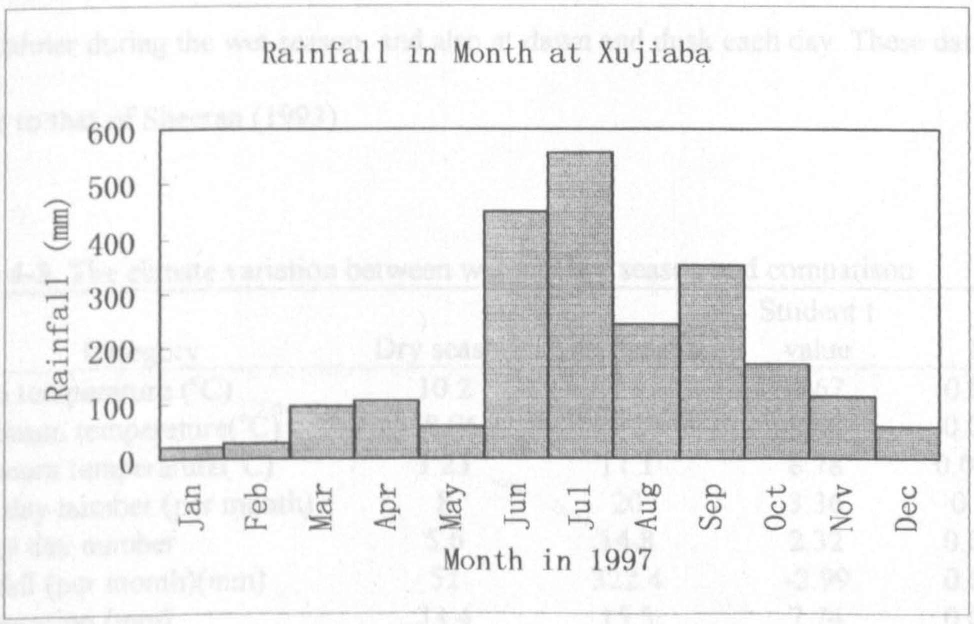


Figure 4-4. The rainfall during 1997 at Xujiaba.

4.3. Temporal and Spatial Climatic Difference Within One Site

Seasonal variation are useful for interpreting gibbons' behaviour. The climate within a local area can vary considerably. Here I present the seasonal variation and data from both inside the forest and at the edge of the forest, mainly based on data from Xiaobahe.

4.3.1. Wet Season *vs.* Dry Season

The wet season is significantly warmer than the dry season at the two sites (**Chapter 4-3**). The other characteristics are always higher in the wet season, except for evaporation. At Xiaobahe, the differences are significant for mean temperature, maximum temperature, and the minimum temperature, number of rain days per month, number of foggy days, rainfall per month (**Table 4-3**). Evaporation was higher in the dry season. Although there were more windy scans in dry season, there was no significant difference in the number of days with strong wind (t=-0.97, P=0.357). Generally, winds were calmer during the wet season, and also at dawn and dusk each day. These data are similar to that of Sheeran (1993).

Table 4-3. The climate variation between wet and dry season and comparison

Category	Dry season	Wet season	Student t value	P
Mean temperature (°C)	10.2	15	4.67	0.002
Maximum temperature(°C)	18.96	16.28	2.48	0.046
Minimum temperature(°C)	3.23	11.1	8.78	0.0001
Rain day number (per month)	8	20	3.36	0.01
Foggy day number	5.6	14.8	2.32	0.047
Rainfall (per month)(mm)	52	322.4	-2.99	0.013
Evaporation (mm)	33.4	15.5	7.74	0.018
Strong windy days (per month)	4	2.33	-0.97	0.357

4.3.2. Forest Edge and Inside of the Forest

The climatic characteristics can be modified by the forest, which might be very important to the animals. At Xiabahe, paired sample t-test showed that the mean temperature is lower inside the forest, compared to that in the open land, but not significantly so. However, both the maximum and the minimum temperatures inside the forest are significantly different from that of the forest edge (**Table 4-4**). The temperature variation within the forest is also smaller than that at the edge of the forest. It is usually about 2 degrees higher or lower than the extreme temperature in the open land. No freezing temperatures have been recorded within the forest. These data show that the forest is an important climate regulator and creates much better micro habitat for its dwellers.

Table 4-4. The climate variation between outside and inside the forest at Xiabahe at about 2230 m asl.

Category	Inside forest	Forest edge	Student t value	P
Mean temperature(°C)	13.6	13.8	1.87	0.079
Maximum temperature(°C)	16.4	18.5	-7.59	0.001
Minimum temperature(°C)	10.7	8.7	6.06	0.001

4.4. Comparison and Discussion

Table 4-5 showed the basic climatic characteristics for several sites of different altitude for different gibbon habitats within China.

Table 4-5. Climates for the several sites where gibbons occurred within China along the altitudinal scale*

Site	Species	Altitude	Average Temperature (°C)	Rainfall (mm)	Extreme. Minimum Temperature (°C)	Extreme Maximum. Temperature (°C).	Source
Nangunhe	Lar	800	21.2	1879	3.5	37	Wang Zhisheng, per. comm.
Bawangling,	Black	1160	19.6	1621	3	30	Liu et al. (1989, 1990)
Jingdong[a]	Possible Black	1170	18.3	1087	-1.4	37.7	Jingdong county Government
Xiaojiangqiao	Possibly Hoolock	1440	16.3	1645	-1.8	31.9	Anomalous (1987)
Daba	Possibly hoolock	1755	15.3	1812	-1.5	28.8	Anonymous (1987)
Jiujie	Possible hoolock	2000	14.9	1715	2.1	30	Anonymous (1987)
Linjiapu	Hoolock	2140	12.8	2499	-1.7	25.9	Anonymous (1987)
Xiaobahe	Black	2230	12.8	2257	-3.3	25.5	Present study
Dafengbao	Hoolock	2400	12.2	2225	-0.5	24.9	Anonymous (1987)
Xujiaba	Black	2460	10.9	2254	-6.2	25.2	Present study
Samaba	Hoolock	2520	10.7	2562	-2.2	23.6	Anonymous (1987)
Zhizhangling	Hoolock	2660	10.7	2570	-1.5	24.5	Anonymous (1987)
Baifengpo	Possible Hoolock	2760	9.5	2440	-1.9	22.1	Anonymous (1987)

*a. Jingdong is based on many years average data. For Xiaobahe and Xujiaba is based on year 1997-1998. For hoolock gibbons' habitat, the data are based on 1981.The minimum and maximum temperature are the extremes.

Based on these data, comparison showed that altitude has a very clear effect on the climate, both on temperature and rainfall (Under 1500 m asl *vs* above 1500 m asl: Mean temperature: t=5.42, P=0.002; Rainfall: t=5.45, P=0.014; Maximum temperature: t=4.14. P=0.013) but not minimum temperature (t=1.69, t=0.155). So the differences between different sites are clearly the effect of altitude: the lower the altitude, the warmer the temperature. For the two main black gibbon study sites in this study, Xiaobahe and Xujiaba, the main trends of the climatic characteristics are similar, but it seems that Xiaobahe, warmer than Xujiaba (pair test: t=2.62, df=11, P=0.024)(but not rainfall: t=-0.218, df=10, P=0.832), may be a better habitat for black gibbons. This is easy to understand since the altitude at Xujiaba is 270 meter higher than Xiaobahe.

Both year 1997 and 1998 were possibly unusual at Xiaobahe and Xujiaba, with much more rain than normal. The yearly rainfall almost reached the highest in the historical records (Zhang, 1987). At Xiaobahe, in 1998, it reached 2025.1mm during the first 9 month so may have exceeded 2200 mm by the end of the year. It was not common in the past for the rainfall to exceed 100 mm in a single day, but in June and August 1998 both at Xujiaba and at Xiaobahe, a single day's rainfall reached to more than 100 mm. Global warming might be the cause of these extreme climatic conditions. In contrast, the year 1992-93 (during the study by Chen (1995)) was a more typical year, with the rainfall a little lower than the average of 1800 mm annually.

It could be that the climatic conditions for black gibbons in Yunnan are really not similar to the other gibbon habitats (see **Appendix 2**). Precipitation is typical of other gibbon habitat (and this might be the main prerequisite for the development of good forest which support the black gibbon populations), but its seasonality of distribution across the year is obvious. The temperatures are much lower in black gibbon habitats, with freezing not uncommon. Although we did not record snowfall (but hail was recorded) at Xiaobahe, snowfall occurred in the habitat of black gibbons at Xujiaba (Chen, 1995). The data show that the habitat of black gibbons suffers a low temperature and extreme temperature variation. Although the temperature in some black gibbon's habitat is cold and can reach freezing point, we should not forget the forest's effect. Minimum temperatures within the forest are significantly warmer, and much suitable for gibbons, compared to those outside the forest. The temperature in the forest is usually more constant and it never reaches freezing point even though it may do so in the top of the canopy.

II. VEGETATION AND FOOD AVAILABILITY

4.5. Overall Picture of Flora and Mid-Mountain Humid Broadleaf Evergreen Forest

Yunnan is diversified in its forest types. In general, only broadleaf evergreen forests support gibbons. In some cases, a few deciduous broad leaf trees and acicular tree (such as *Pinus*) occur in the gibbon's habitats, especially in those areas subject to disturbance. The broadleaf evergreen forest can be divided into several types based on the species composition, seasonal appearance and environmental characteristics, such as rain forest, humid and semi-humid, monsoon and mountainous forest (Wu *et al.*, 1987).

The broadleaf evergreen forests exhibit zonal differentiation along the mountain slopes. These forests are called, from bottom to top, south subtropical semi-humid monsoon evergreen broadleaf forest (up to 1700m), middle subtropical humid monsoon evergreen broadleaf forest (from 1700 to 2200m), north subtropical humid monsoon evergreen broadleaf forest (from 2200- 2600), and finally on the higher slopes is warm temperate humid monsoon broadleaf evergreen forest (Anonymous, 1960; Liu *et al.*, 1989; Peng and Wu, 1997).

In most mountain ranges or mountains, most primary vegetation under 2000 m has been converted by human activity to pine tree forest, grassland, shrub, and other secondary vegetation now. The practices of slash-and-burn agriculture, clearing of forest for terracing and rice paddies, over-grazing by domesticated animals, and erosion have all exacted a toll on the surrounding area, reducing its carrying capacity for wildlife (Zhang *et al.*, 1981). Above 2000 m, the vegetation has been significantly altered, but some of the primary evergreen broad-leaf forest remains and supports gibbon populations. At present, the main forest types which support black gibbons are called mid-mountain humid evergreen broadleaf forest (Jin, 1979; Wu *et al.*, 1987; Anonymous, 1987).

This forest, located on the top of the mountains, is obviously a little more like temperate forest, although it is, on geographical grounds, categorized as subtropical (Jin, 1979). In both Wuliang Mts and Ailao Mts. reserves, forests are mainly of this type. In these two nature reserves, the gibbons have been recorded only above 1800 meters, and usually above 2100 m.

Mid-mountain Humid Broadleaf Evergreen Forest

The canopy of this type of forest is continuous, with few gaps. Unlike tropical rainforest in Southeast Asia, there was only one upper canopy layer, and no emergent canopy layer. The canopy height varied, from 10 to about 30 meters and averaged 24 m among the forest that remained (Liu *et al.*, 1989; Peng, 1997).

The composition of the forest is not as diverse as the tropical rainforest of other gibbon species. Most trees belong to a few families, such as Fagaceae, Lauraceae, Theaceae and Magnoliaceae. The most prominent family is usually Fagaceae, with the highest basal area among all families.

In those remaining forests with least disturbance, fig trees are very rare or absent (Anonymous, 1960; Chen, 1995; You, 1987). However, figs are available at some sites, though at very low density (Lan, 1995; You, 1987). The reason for the presence of figs in these sites is unclear, but habitat with disturbance might enrich the abundance of the fig tree. The fig tree is not good wood for any human purpose, and local people usually do not collect them for any other reasons. So it is unlikely that human cutting have been responsible for eradicating figs in the forest.

The climbers vary in term of species, number and individuals at different sites, although it seems climbers are less common in climax forests with no disturbance (Anonymous, 1960; You, 1987). However, the edge of the forest, which is subject to severe human disturbance, showed a much greater abundance of liana species.

Owing to the marked dry and wet seasonality, the forests showed extensive phenological variations, including defoliation in the cold mid-dry season.

4.6. Xiaobahe and Habitat of Group B, Wuliang Mts.

At Xiabahe, there is some difference in the forest composition and structure between habitat of each group (*i.e.*, group B, F, G, and C and others), but the basic forest characters, like species composition, are much similar to each other if checked with other sites (**Table 4-6**). In the following paragraphs, I present the data for habitat of group B, for some difference of other groups, I will noted in the text.

Table 4-6. The main 10 species of importance in the habitat of each groups based on individual numbers*.

Group B	Group F[a]	Group G	KNH	Xujiaba (Chen, 1995)
Laurocerasus phaeosticta	*Lithocarpus xylocarpus*	*Laurocerasus phaeosticta*	*Schimma noronhae*	*Schima noronhae*
Lithocarpus xylocarpus	*Laurocerasus phaeosticta*	*Hartia chinensis*	*Cerasus cerasiodes*	*Vaccinium mandarinorum*
Machilus bombycina	*Acer heptalobum*	*Vaccinium mandarinorum*	*Cinnamonmen*	*Lithocarpus chintungensis*
Manglietia insignis	*Mangnoliatus insignis*	*Lithocarpus xylocarpus*	*Betula alnoides*	*Lithocarpus xylocarpus*
Vaccinium mandarinorum	*Prunus majestica*	*Machilus bombycina*	*Lyonia ovfolia*	*Hartia sinensis*
Lithocarpus truncatus	*Rhododendren* sp.	*Castonopsis orthacantha*	*Castonopsis*	*Ilex micrococca*
Meliosma kirkii	*Machilus bombycina*	*Acer heptalobum*	*Juglan*	*Lyonia ovalifolia*
Machilus viridis	*Lithocarpus truncatus*	*Gyntotema*	*Phoebe*	*Rododendron leptothrium*
Castanopsis orthacantha	*Ficus sp.*	*Rhododendron*		*Castanopsis wattii*
Cyclobalanopsis glaucoides	*Machinus viridis*	*Rhododendron*		*Illicium macranthum*

*a. Based on 7 20x20 m^2 plots sampled in 1994.

4.6.1. Canopy, Tree Size and Density

In general, the canopy was continuous, although forest gaps existed. Of the 360 points we checked, only 14 points were found covered by no canopy directly over head (3.9%). There is only one upper canopy layer and no emergent layer (**Figures 4-5** and **4-6**). The canopy height has the following descriptive statistics: Maximum=31 m; mode=23 meters; median=20m, and mean=20.3 m (n=120, SD=5.0). These figure were all smaller than at Xujiaba (Chen, 1995).

All the trees with DBH>=10 cm were measured in twenty 20x50 m^2 plots in the home range of the main study group B. The average DBH is 27.14cm (n=780, SD=16.56). Most tree were small with diameters between 10 to 50 cm (**Figure 4-7**). There were 345 tree (44.2%) in the 20 plots with a diameter between 10 and 20 cm. DBH of 90% of trees was no larger than 50 cm. Big trees were scarce: there were only 78 trees with DBH> 50 (10 % of total). Only 3 trees had DBH> 100 cm. Largest DBH found was 147 cm. Tree density is 390 tree/ha. Basal area can be expressed as per tree or per plot (1000 m^2). The average basal area per tree is 793.9 cm^2 (n=780, SD=1148). The sum of tree basal area averaged 30.97 m^2 per ha.

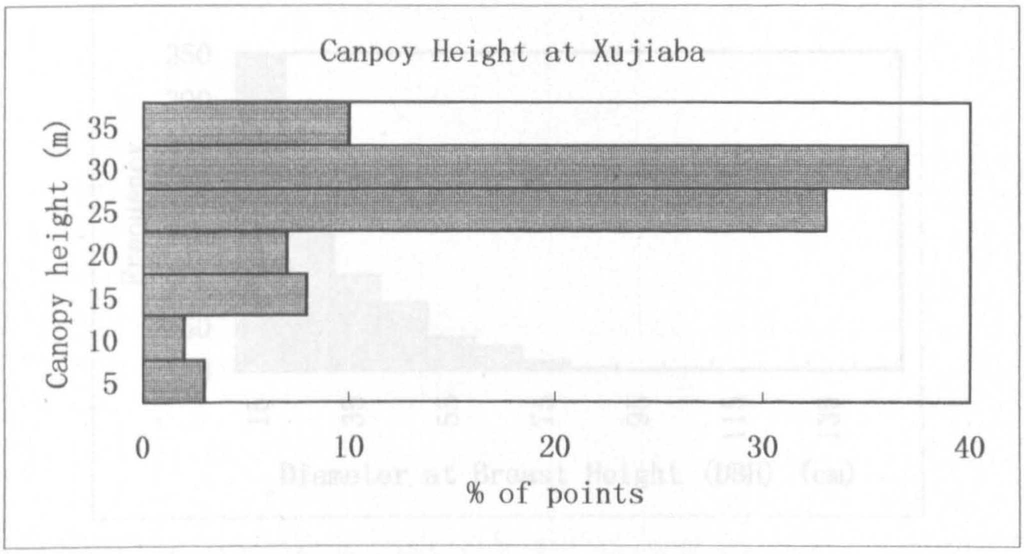


Figure 4-5. Distribution of canopy height at Xujiaba (data from Chen, 1995)

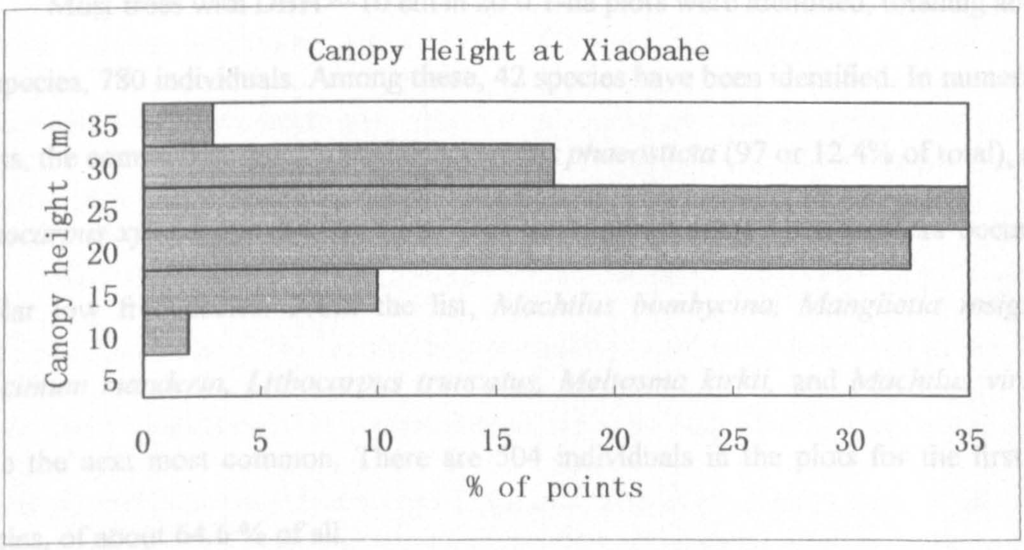


Figure 4-6. Distribution of canopy height at Xiaobahe (Group B).

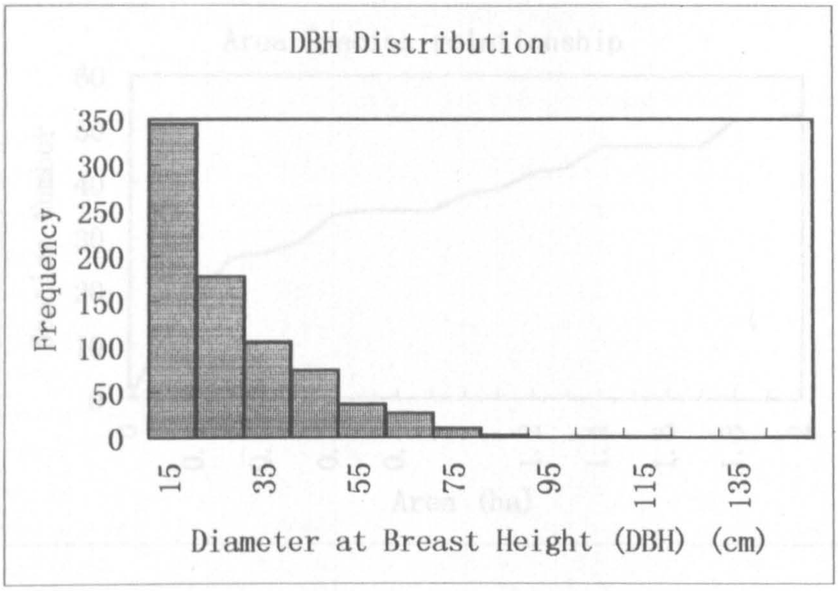


Figure 4-7.Distribution of the tree diameter (DBH) in the habitat of group B.

4.6.2. Species Composition

Most trees with DBH>=10 cm in 20 0.1-ha plots were identified, totalling about 50 species, 780 individuals. Among these, 42 species have been identified. In numerical terms, the commonest species are *Laurocerasus phaeosticta* (97 or 12.4% of total), and *Lithocarpus xylocarpys* (84, or 10.8 % of total individuals). All the others occur at similar low frequencies. From the list, *Machilus bombycina, Manglietia insignis, Vaccinium manderin, Lithocarpus truncatus, Meliosma kirkii,* and *Machilus viridis* were the next most common. There are 504 individuals in the plots for the first 10 species, of about 64.6 % of all.

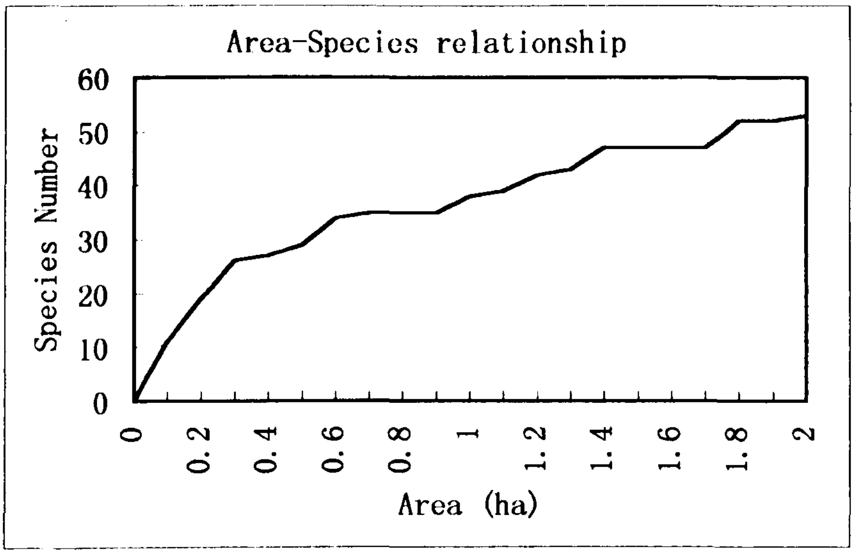


Figure 4-8. The area-species numbers within the habitat of group B.

Twenty-four out of a total 50 species were represented by less than 10 individuals each, and 6 of these species were represented each by only one individual. The species-area relationship curve shown in **Figure 4-8** suggests that most of the species of plants may have been discovered. However, not all species have been recorded, since the survey on the plant community is very complicated.

All trees identified belong to 42 species of 19 families. Fagaceae (198), Rosaceae (131) and Lauraceae (115) are the largest families in terms of individual stems. The fourth commonest family is Magnoliaceae with 54 individuals. The single most prominent and important family was Fagaceae. The sum of basal area of all trees belonging to this family was 24.44 m^2(41.3%), while the total basal area of all the other families was only 37.49 m^2 (58.7%). The two most prominent species were from this family, namely *Lithocarpus xylocarpus* and *Lithoccarpus truncatus*. The summary of the family list and their stem frequency and basal cover for the plots from Group B (Xiaobahe) and group AC2 (Xujiaba, after Chen, 1995) are given in **Tables 4-7** and **4-8**.

Table 4-7. The species numbers, basal cover, individual numbers of each family within the home range of group B at Xiaobahe.

Family	Basal cover (m^2)	Total number of individual	Species number
Fagaceae	24.44	194	5
Lauraceae	9.87	114	6
Rosaceae	7.38	138	4
Meliosmaceae	4.71	40	1
Magnoliaceae	4.11	49	2
Betulaceae	2.18	10	2
Theaceae	1.84	36	6
Eleaocarpaceae	1.40	15	1
Aceraceae	1.33	21	1
Ericaceae	0.84	36	3
Aquifoliaceae	0.82	23	2
Vacciniaceae	0.70	48	1
Symplocaceae	0.55	21	1
Moraceae	0.33	3	1
Euphorbiaceae	0.22	4	1
Illiciaceae	0.18	6	1
Rutaceae	0.13	1	1
Styraceae	0.09	4	1
Buddlejaceae	0.03	2	1
Myricaceae	0.02	2	1
Unknown	0.76	13	c.a.8
Total	61.93	780	50

Table 4-8. The species numbers, basal cover, individual numbers of each family within the home range of group AC2 at Xujiabah (data from Chen, 1995)

Family	Basal cover (m^2)	Total number of individual	Species number
Fagaceae	86.5	619	6
Theaceae	22.6	444	6
Ericaceae	7.0	267	4
Aquifoliaceae	6.4	180	4
Magnoliaceae	6.1	126	2
Lauraceae	5.9	142	8
Araliaceae	4.3	74	3
Vacciniaceae	3.4	211	1
Illiciaceae	3.2	106	1
Rosaceae	2.5	85	4
Aceraceae	1.3	33	1
Symplocaceae	0.9	33	4
Betulaceae.	0.5	5	1
Styracaceae	0.3	14	1
Dichapetaliaceae	0.3	4	1
Pinaceae.	0.3	1	1
Tetracentraceae	0.2	2	1
Oleaceae	0.0	2	1
Calicaceae	0.0	1	1
Total	152.19	2349	51

Some shrubs or tree which are important food species to group B have not been recorded in those plots. They are usually along the edges of the good forest patches, and when food available, the group B used intensively. I have checked some individuals and estimated stem density along the home range of group B, measuring their diameters and counting their numbers (**Table 4-9**), and using these data to calculate the food availability.

At Xiaobahe, the figs (*Ficus*) did occur but with low density, about 0.385% (3 individuals) individuals in the 2 ha samples, taking 25th place of all species. Its individual density is 1.5 individuals per hectare.

Table 4-9. The species of important value to gibbons which are not presented in 20 plots and its estimated density and ecological parameters randomly measured.

Family	Latin name	Items counted and/or measured	Density estimated (stems/ha)	Averaged dbh (cm)	Averaged basal cover (cm^2)
Meliosmaceae	*Meliosma dumicola*	5	2	15.68	193.16
Anacardiaceae	*Rhus chinensis*	5	1	13.46	284.46
Myricaceae	*Myrica esculenta*	5	1	24.67	956.34
Ericadeae	*Rhododendron delavayi*	5	2	25.44	1016.35
Lauraceae	*Litsea cubeba*	5	1	11.0	190.23
Loranthaceae[a]	Spp.	8	24	?	?

*a. a parasitic species group, scattered on trees such as *Betula luminifera* and species from Fagaceae. They are small scrubs, no diameter data.

The forest of the whole Xiaobahe district is in general similar to the characteristics of the habitat of group B which have been presented in the previous sections. However, there are also some differences between them. In structural terms, the forest of group F and G's habitat are more continuous. None of these differences are of great significance.

4.7. Habitats of Other Groups and Sites

Besides the habitat of Group B, F and G at Xiaobahe, I also have samples for the habitats of group KNH at Kainanhe and for sites at Xujiaba, and for hoolock gibbons in west Yunnan. Data for Xujiaba are based on line plot methods (See **Chapter 2** for detail). Here I present the general characters of the habitats of these groups or sites, and then some comparison and discussion (**Table 4-10**).

4.7.1. Kainanhe

The habitat of group KNH is different from that of Xiabahe, since the altitude is only 1700 to 1900 m, about 300-500 m lower. The habitat experiences a different climate. The composition of the tree species is different, with more species of a tropical character (**Table 4-6**). Owing to more human disturbances, the canopy is not so continuous in where forest left, and more deciduous and coniferous species, like pine tree are available. Shrubs are prevalent under the forest, with a lot of small lianas. Trees are also small in general.

Table 4-10. Tree stem density at several sites*

Site and/or Group	Xiaobahe and near						Xu-jiaba[b]	Lingcang Daxueshan
	B (1997-1998)	B (1994)	F	G	Xiaobahe all[a]	KNH		
Sample areas(ha)	2	0.28	0.28	0.28	0.48	0.36	3	0.12
Tree density (stem/ha)	390	571	550	703	511	569	783	613

*a. Based on 20x20 m^2 samples either from 1994 (group B, F) and 1998 (group G) survey. b. Data from Chen (1995).

4.7.2. Xujiaba

Chen (1995) has provided a detailed description of the habitat of the gibbon group he studied. The average canopy looks a little bit higher (**Figure 4-5**), the tree stem density is higher than that of Xiaobahe and Kainnanhe. But the averaged tree DBH is smaller, and with less shrubs under the canopy, and with less deciduous species

4.8. Diversity and Comparison

4.8.1. Tree Diversity

Canopy Height and DBH

For these sites mentioned above, the canopy heights are different in each site, but all of them have only one main canopy layer (**Figures 4-5, 4-6**), about 20 to 28 meters above the ground. Disturbed forest showed more unclear canopy layers, as at Xiabahe and Kainanhe, compared to Xujiaba, where the forest is in good condition (little disturbance). But compared to the habitats in tropical rain-forest, all forest occupied by black gibbons are relatively simple, with fewer layers (*e.g.* Hainan Is., Liu and Jing, 1990).

The averaged DBH of trees in group B's habitat seems larger than that of AC2 of Chen at Xujiaba. But based on our circle plot sampling (at Xujiaba, mainly located at group F's home range), trees are significantly larger at Xujiaba than at Xiaobahe (Mann-Whitney test, U=256.7, P=0.008, total 248 tree stems). Both canopy height and DBH might not account the important habitat difference to black gibbons for the two sites.

Species Composition

It is very difficult to compare the habitat differences in floral diversity between sites, though the differences exist and are possibly significant, owing to the different method used and areas sampled. The complexity of the habitat should be the main reason for the difficulties. However, some relative index can be used to compare the habitats. Based on intuitive biological understanding, a good habitat to gibbons should have more (preferred) food species and individual trees, and a complex physical forest structure such as continuous canopy, high and dense crown cover, high canopy, moderate sized twigs with moderate density (but not too dense). In contrast, a poor quality habitat will only have a few food species and few individual trees, with lower canopy, small dense twigs and so on. High diversity and high evenness usually represent high and even food availability. High evenness is especially important for the gibbons to deal with the food shortage in some hard seasons (such as dry seasons). Based on the plot sampled, we can calculate Simpson's diversity index for each site (Begon *et al.*, 1990). The formula is as follows

$$H=-\Sigma(p_i)\ln(p_i)$$

and, from this, the evenness index:

$$E=H/H_{max} \quad \text{and}$$

$$H_{max}=\mathrm{Ln}S$$

Where H is the Simpson diversity index, and E is the evenness, H_{max} is the maximum H, S is the total species number, p_i is the proportion of *i* species of all individuals.

Based on the line point method, we can calculate the index for the comparison between Xiaobahe and Xujiaba. At Xiaobahe, the tree diversity index is H=3.2, higher than that of Xujiaba (H=2.98). That means that diversity of species composition at Xiaobahe is more complex, though only marginally so.

Table 4-11. The floral diversity index in several sites based on different methods

Habitat	No. of plots (m^2)	Diversity index	Evenness	Sources
Xiaibahe				
1).Xiaobahe (fir all BFG groups)[a]	24(400)	3.40036	0.86483	This study
2). Xiaobahe[b]	27 points	3.0507	0.90148	This study
3) Group B	20(1000)	3.22944	0.82552	This study
4) Group B	7(400)	3.19153	0.90505	This study
5) Group F	7(400)	2.9089	0.83933	This study
6) Group G	7(400)	3.1891	0.88994	This study
Kainanhe	9 (400)	3.31985	0.85758	This study
Xujiaba				
1) Group AC2	3(10000)	3.12396	0.79453	Chen (1995)
2) Xujiaba	31 points	2.99652	0.88989	This study
Daxueshan (Lingcang)	3(400)	2.89353	0.91047	This study

* a. Xiaobahe (1) is by the all plots ($400m^2$) from B, F (1994) and G (1998) together for calculation, and (2) is by the circle plot tree survey, mainly in the range of group F. Xujiaba (1) Group AC2 are based on the data of Chen (1995); (2) is for the circle plot survey in 1998. Daxueshan is a similar forest habitat among the black gibbon distribution range, but no gibbons found recently.

Table 4-12. The species diversity comparison between habitat of each group based on the plots sampling at Xiaobahe.

	B(1)	B(2)	F	G
H	3.19153	3.2944	2.9089	3.1891
E	0.90505	0.82552	0.83933	0.88994
Species number	34	50	32	36
Total tree individuals	165	780	188	198

B(1) is based on 7 20x20 m^2 plots; B(2) is based on 20 20x50 m^2 plots.

Table 4-13. The tree diversity index between different sites based on several study.

Site	Xiaobahe(1)	Xiaobahe(2)	Xujiaba(1)	Xujiaba (2)	Daxueshan
H	3.20507	3.32	2.99652	3.12396	2.89353
E	0.90148	0.8623	0.88989	0.79453	0.91047
Species number	36	47	29	51	24
Total tree individuals	108	551	124	2349	92

* Xiaobahe(1) is by the circle plot tree survey, (2) is by the all plots ($400m^2$) from B, F (1994) and G (1998) together for calculation.
Xujiaba (1) is for the circle plot survey, Xujiaba (2) are based on the data of Chen (1995).

Table 4-14. The tree diversity index between the habitat of groups: Xiaobahe (Group B) and Xujiaba (AC2).

Site and Group	Xiaobahe (Group B)	Xujiaba (Group AC2)
Diversity Index (H)	3.22944	3.12396
Evenness (E)	0.82552	0.79453

From the **Tables (4-11 to 4-14)** above, we can see, in general, the diversity index is usually higher at Xiaobahe than at Xujiaba. The evenness is also higher at Xiaobahe. This means that food availability is likely to be more abundant and evenly distributed at Xiaobahe than at Xijiaba. The best habitat might be that of group B, according to the index, and the forest at Daxueshan (without gibbons at present) seems the worst in diversity and this might reflect the habitat deterioration there and the cause of the disappearance of black gibbons there some time ago.

4.8.2. Liana Diversity

Liana species play an important role in black gibbon diet. The gibbons also used it as means and support during travel. The juveniles and infants used to play on them, too. However, we consider their importance because they provide food for gibbons. Most of them are food species.

Not all vine species reach to the canopy. Only those woody climbers that reach to the canopy, where the black gibbons usually spend more time, can be used by gibbon group members. So our work concentrated on those woody climbers. All individuals measured and listed are those that actually reach the canopy layer.

Species Composition and Abundance

There is a difference in liana species among the habitats of each gibbon group or two sites, or between two species (*H. concolor* in middle Yunnan and *H. hoolock* in west Yunnan), but some similar species are present at all sites (**Table 4-15**, either based on group and based on sites). Some quantitative data for different habitats of black gibbons are showed in **Table 4-16**.

Table 4-15. The liana species for the black and hoolock gibbons' habitat in Yunnan*.

	Group (1) or Sites (2)							
	Black gibbon					Hoolock gibbon		
Species	B^1	F^1	G^1	KNH$^{1\&2}$	XJB^2	MLH^2	HNT^2	PH^2
Actinidia sp. (*e.g. glaucocallosa*)	+	+	+		+	+	+	+
Holboellia fargesii	+	+			+	+		
Millettia pachycarpa	+							
Parthenocissus himalayana	+	+		+	+	+		
Celastrus monospermus	+	+	+			+		
Rubus spp.	+	+	+		+	+		+
Kadsura coccinea	+	+	+		+	+	+	+
Toddalia asiatica	+	+						
Jasminum duclousii	+	+						
Melodinus khasianus	+	+						
Millettia dielsiana	+							
Elaeagnus conferta	+	+			+			+
Rosa longicuspis	+	+			+	+	+	+
Dalbergia spp.	+							
Ficus spp.		+		+				

*For sites: KNH (Kainanhe); MLH (Mulonghe), HNT(Heinitang), PH(Pinghe). 1, gibbon group code, 2, site code.

Table 4-16. The liana characteristics for different sites.

Site and Group	Xiaobahe			Kainanhe
	B	F	G	KNH
Plot number	7	7	7	9
Stem density(per 100 m^2)	3.718	2.2	1.0	0.5
Food individual density (per ha)	2.25	1.2	0.86	0.22
Total liana in plots	70	69	29	18
Species number	10	8	10	5
Possible food species	7	6	7	2
Possible food individuals	63	61	25	7
Liana appeared plots	7/8	8/8	7/8	4/9
food vines in plots	7/8	8/8	7/8	4/9
Maximum ind. per plot	28	18	13	8

Group B's Habitat

The climbers belong to more than 15 species, totalling 466 individuals in 17 plots (density of 274 individuals/ha, or 2.74 ind/100m^2). Among 15 species (taxa), only 2 to 3 showed deciduous characteristics, most being evergreen species. *Actinidia* spp (at least two species) have most individuals, and is the most common and popular food species for gibbons; they occurred in most plots (85%); then is the *Kadsura coccinea* (60%) and *Holboellia* spp.(70%). All of these are very important food species for the gibbons. We here refer to them as three main liana species (taxa) for gibbons. Another prominent species is *Celastrus monospermus*, occurring in 75% plots.

Group F and Group G

Group F's home range also has abundant liana resources. In seven plots within its home range, we counted 69 individuals, belongs to 8 species, with a density of 2.2 ind/ 100 m^2. The species recorded are similar, about 12 species. For the three main liana taxa (*Actinidia* spp group, *Holboellia* spp group and *Kadsura* spp. group), the abundance is quite similar. *Toddalia asiatica* is much more abundant in the home range, if compared with that of B and G.

Within the home range of group G, the liana density is 1 individual per 100 m^2, and about 10 species. Some species, especially three most important taxa groups, are not so abundant, especially *Holboellia fargesii*. Other species are similar. About 10 species are found within the home range. Only one species did not occur in the home range of Group B, *Zanthoxyclus*. It is a possible food species to black gibbons, too, although we have no evidence from direct observations of wild gibbon. It is not a very important species, since there were few individuals of this species available in the forest around the Xiaobahe.

Kainanhe

Liana are rare at Kainanhe: both numbers of species and individuals are low. There are only 18 individuals belonging to 5 species among nine 20x20 m^2 area, with a density of 0.5 individuals per 100 m^2. The most common species is *Pueraria omeiensis*, which belongs to the Papilionaceae and possibly not a food provider for gibbons (at least, according to the local people). The average diameters is 10.3±7.3 cm (n=18), bigger than the liana average at Xiaobahe (the liana diameter within the group G's home range is 6.2±3.04 cm (n=29).

4.8.3. Comparison of Liana Abundance

Comparison Between Groups in the Same Subpopulation (Mt. Wuliang)

The comparisons between the habitat of each group are based on the vine numbers per (20x 20 m^2) plot. There is a significant difference in the liana density between groups B, F, G and KNH (Kruskal-Wallis H test, $X^2=12.411$, df=3, P=0.006). The vine density for B and F is high, and that for G and KNH lower. That might be related to the habitat quality.

Comparison Between Populations (Wuliang Mts. *vs*. Ailao Mts.)

In order to compare the liana differences between the two mountains --- Mts. Wuliang and Mts. Ailao, especially between Xiaobahe (Wuliang) and Xujiaba (Ailao)--- I compared 34 plots at Xiaobahe and 31 plots at Xujiaba. All the plots are circles of 20 m in diameter, along six and nine 200-meters long transects. Plots are 50 or more meters apart. Results showed that the liana density is high at Xiaobahe (233.6 individuals per ha), but very low at Xujiaba (only 29.6/ha). The significant difference is highly significant (Mann-Whitney test, U=367.85, n_1=30, n_2=31, P<0.001).

Comparison Between Habitat of Different Hylobatid Species

Comparison of the liana data from Xiaobahe with data from Mulonghe, a good habitat for hoolock gibbons in west Yunnan (Lan *et al.*, 1995), yield a significant difference (Mann-Whitney test, U=268.82, P=0.024). When we group data according to sites, the difference in liana abundance is still present (for Xiabahe, Kainanhe, Mulonghe, Heinitang, Pinghe, Kruskal-Wallis H test, X^2=13.376, df=4, P=0.01).

4.9. Seasonal Variation of Food availability

4.9.1. Food Availability Index

To provide a measure of food availability (in m^2 basal area per hectare), I used the following index:

$$Ni*LDi*(BAi*PSi)*Ai.$$

Where:

Ni is the percentage of number of plots in which species i is found

LDi is the local density of species i along those plots

Bai is the mean basal area for all individuals of species i

Psi is the mean phenology score for individuals of species i

and Ai is the proportion of individuals of species i that are in fruit/flowering.

This index is a modified version of one used by Harrison (1984) in a study of Senegal green monkeys (Barrett, 1995). It differs in that patch size was indexed by using (Bai*Psi), rather than canopy volume. This index was selected because it incorporates measures of spatial dispersion (Ni and LDi), patch size (BAi*PSi) and species synchrony (Ai), and thus captures something of the dynamic nature of phenologcial patterns within the forest. Basal area is used as a measure of tree size since this has been shown to be related to crown volume (Whitmore, 1975, 1990) and therefore production capacity.

The difference here from Barrett (1995) is that: Ni is the percentage of the number of plots in which species i is found, and BAi is the mean basal area for all individuals of species i, because usually all individuals of the same species are of similar phenology, and we did not check all individuals in all plots since it was impossible to do so. PSi is the mean phenology score for individuals based on 5 individuals sampled twice a month, Ai is the proportion of individuals of species that are in fruiting or with young leaves or in flowering based on the 5 individuals (10 samples per month).

Data on the availability of fruits, young leaves and flowers are not presented in the analyses of all tree species and shrub or liana species. Preliminary analysis of the feeding revealed that most common tree species are of no food value for gibbons (*e.g.* 72.5% of the basal area of the first 7 species in Chen (1995) are not eaten by black gibbons). So I just include those species that we have observed to be food species. The list is provided in **Table 4-17.**

Table 4-17. The list of plant species included in the food availability analysis at Xiaobahe.

Latin name	Number in 2 ha sampled
Betula luminifera	5
Cerasus cerasiodes	6
Spp. of Loranthaceae	48
Ficus virens	3
Elaeagnus spp.	1
Mallotus philippinensis	4
Rhododendron delavayi	3
Myrica esculenta	16
Rhus chinensis	4
Michelia floribunda	1
Actinida spp.	122
Elaeocarpus braceanus	15
Kedsura coccinea	70
Holboellia forgesii	69
Rhododendron decorum	3
Cinnamomum tamala	7
Celastrus glaucophyllus	60
Litsea cubeba	12
Manglietia insignis	48
Meliosma kirkii	40
Prunus majestica	17
Lyonia ovalifolia	20
Vaccinium mandarinorum	48
Castanopsis orthacantha	29

Mature leaf availability is not presented since there is insignificant variation among most trees, although leaves are an important part of the gibbons' diet. The high availability of mature leaves is not expected to influence gibbons foraging behaviour a lot: leaves are just used to compensate for the shortage of other food items. So I excluded information on mature leaves. Analysis of the phenology data revealed that over 80% of the sample species were recorded as having at least some mature leaves each month. Food availability measures were therefore concentrated on reproductive parts, *i.e.* fruit (ripe and unripe), flowers, and flower buds, and young leaves.

4.9.2. Seasonal Variation of Food Availability

Within the habitat of group B at Xiaobahe, it seems that fruit availability is poor during dry season, especially late dry season, such as from March and April, and abundant during wet season to early dry season (**Figure 4-9**). But the ripe fruit are much abundant during late wet season to early dry season, in autumn (**Figure 4-10**). Both young leaves and flowers are much more abundant during late dry season to middle wet season (young leaves: **Figure 4-11;** flowers: **Figure 4-12**), but flowers become to be abundant two months late and reach its highest points one month late.

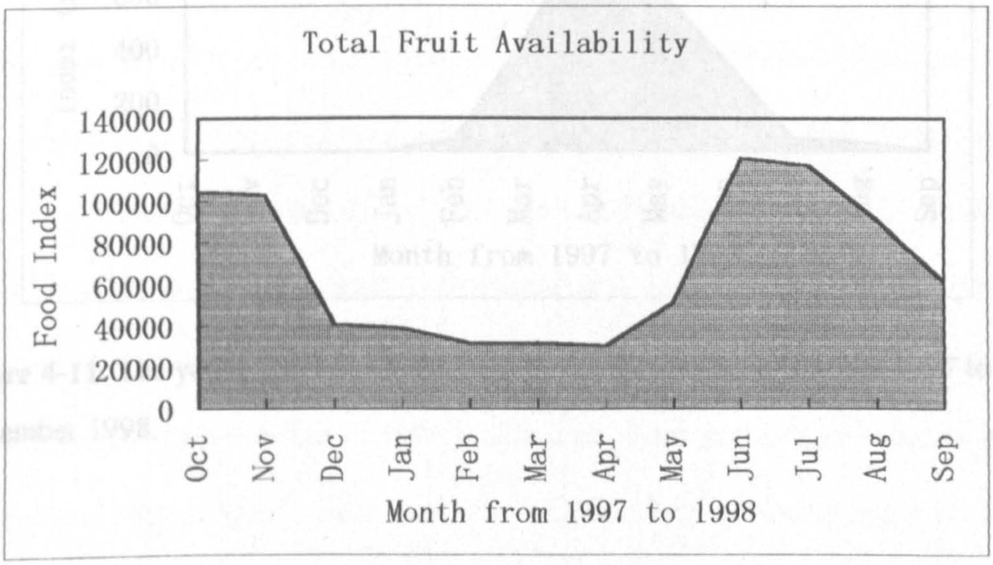


Figure 4-9. Fruit availability in the year from October 1997 to September 1998.

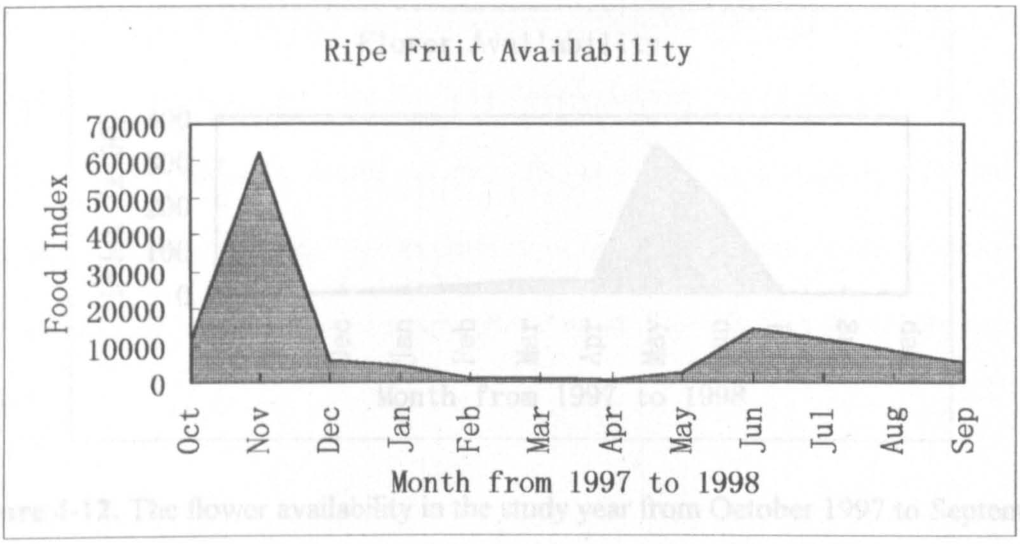


Figure 4-10. Ripe fruit availability from 1997 to 1998.

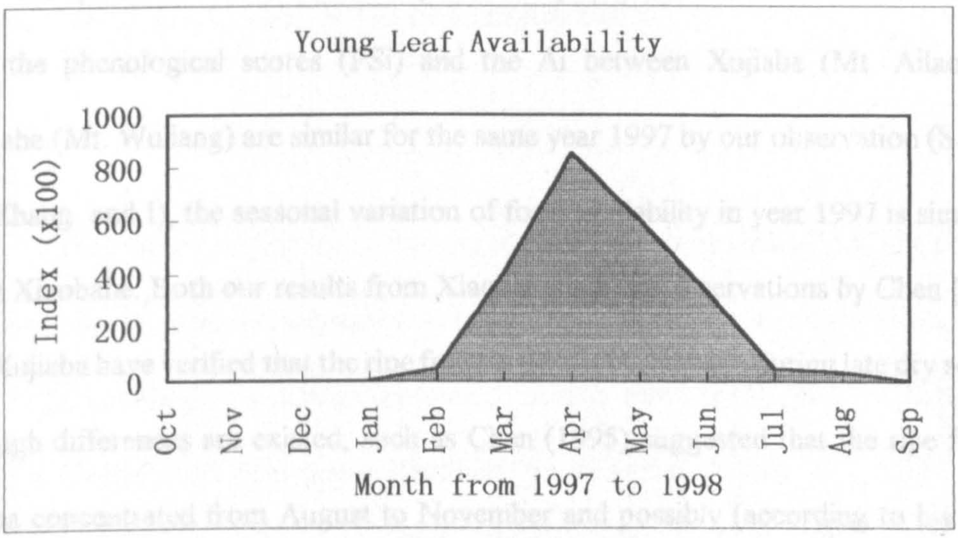


Figure 4-11. The young leaves availability in the study year from October 1997 to September 1998.

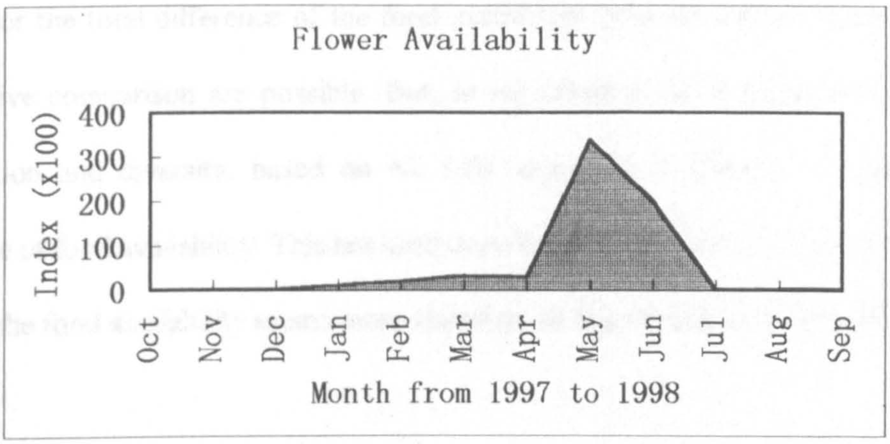


Figure 4-12. The flower availability in the study year from October 1997 to September 1998.

No quantitative food availability data are presented here for habitat at Xujiaba. Since the phenological scores (PSi) and the Ai between Xujiaba (Mt. Ailao) and Xiaobahe (Mt. Wuliang) are similar for the same year 1997 by our observation (S.C. Li, X. J. Zhang and I), the seasonal variation of food availability in year 1997 is similar to that at Xiaobahe. Both our results from Xiaobahe and the observations by Chen (1995) from Xujiaba have verified that the ripe fruits are most in shortage during late dry season. Although differences are existed, such as Chen (1995) suggested that the ripe fruit at Xujiaba concentrated from August to November and possibly (according to his figure 23) reach its highest in September and October, but that is from June to November and reach its highest in November in 1997 at Xiaobahe, most phenological records are in similar trend. Phenological yearly variation and plant fruiting rhythm might cause the difference. At Xiaobahe, it can be found, as shown in **Figure 4-12**, the ripe fruit availability are possibly different for the year 1997 and 1998. Quite a lot of species, including important gibbon food species, showed the fruiting differences from year to year. More details will be discussed in feeding chapter.

For the total difference of the food availability between the two sites, now no quantitative comparison are possible. But, in my opinion, the comparison of species composition and diversity, based on Ni, LDi, and BAi, is enough to evaluate the difference of food availability. This has been done by previous sections. As it is shown, in general, the food availability seems more abundant at Xiaobahe than at Xujiaba, in most seasons.

4.10. Discussion

From data above, we can see that the habitat characteristics of black gibbons are very complicated. Each habitat has its own characteristics.

Climates

In most habitat of gibbons in Yunnan, altitude has a very clear effect, and possibly main effect on the climates, especially on temperature. Although the main trends of the climatic characteristics are similar between Xiaobahe and Xujiaba, the temperature at Xujiaba is always lower than that at Xiaobahe, for its higher altitude.

Precipitation in Yunnan are typical of other gibbon habitat, but its seasonality of distribution across the year is obviously different from that of most other gibbons. The temperatures are much lower in black gibbon habitats, sometimes reaching freezing point or lower. This kind of climatic profile might have important effects on the behavioural ecology of black gibbons through thermoregulation, behaviour adaptation like sun bathing in early morning and food availability. However, forest itself has good effect to modify the unsuitable temperature profile for gibbons. Minimum temperatures within the forest are significantly warmer, and much suitable for gibbons, compared to those outside the forest. The temperature in the forest is usually more constant and it never reaches freezing point even though it may do so in the top of the canopy.

Vegetation

Although it is difficult to compare the habitat differences between sites, owing to the different methods used, areas sampled, as well as the complexity of the habitats, we found that the structure and composition of the forest are still different from one site to another. Compared to the habitats of gibbons in tropical rainforest (like Hainan black gibbons, Liu and Jin, 1990), forest occupied by black gibbons in Yunnan are relatively simple, with fewer layers, or only one main layer, although the canopy heights may be different from each other. In contrast, the disturbed habitat at Xiaobahe has more canopy layers, but not a complete continuous main canopy, and the trees are smaller. However, we found that these habitats, at least within the homer range of some groups, seem to be good gibbon habitat, with more (preferred) food species, compared with some no or less disturbed habitats like those at Xujiaba.

There is a difference in liana species among the habitats of each gibbon group and between two species (*H. concolor* in central Yunnan and *H. hoolock* in west Yunnan), but some species are present at most habitats in high altitude. For black gibbons, three important food taxa (*Actinidia* spp, at least two species; *Kadsura coccinea* and *Holboellia* spp.) are usually abundant. Some other species differences are also important as they are good food species too. These liana species might be the key to the gibbons ability to survive there. The habitats of some groups (like B, F, in some period multi-female groups found) are rich in liana species and number, but the other sites (usually only one-female groups found), including the Xujiaba and west Yunnan hoolock's habitats, have few liana species and lower number per capita area.

Food Availability

In the habitats of black gibbons in Yunnan, fruit availability is poor during dry season, especially late dry season, and abundant during wet season to early dry season. The ripe fruits, maybe with a different trend in availability to that of total fruits, are abundant during late wet season to early dry season, in autumn. Both young leaves and flowers are much more abundant during late dry season to middle wet season, with the peak time of difference. The main influence are the climate variables, mainly the temperature and rainfall. The general seasonal variation are also important, or it is the basic cause of all climatic periodical variation, which influence the vegetation's periodic variation finally influence the seasonal food availability.

CHAPTER 5. ACTIVITY PATTERN AND TIME BUDGET

5.1. Introduction

In this chapter, I attempt to characterise the activity pattern, time budget and related behaviour of black gibbon. Following a brief review of the methods used to measure certain behavioural variables (5.2), I go on to describe activity patterns, time budget and monthly variation (5.3) relationship with group size (5.4.) and diurnal Activity variation (5.5.), difference between age-sex group (5.6.) and summary (5.7).

5.2. Method

5.2.1. Definition

The time when the first member of the observed group left its sleeping tree was taken as the start of the activity period. Once all members are in the sleeping tree and no more activity except rest happened, the last records of a member travelling or feeding was taken as the end of the activity period. Following Gittins (1982), the time of dawn was recorded as the time when canopy tree leaf colour about 50 to 200 meters away was discernible.

5.2.2. Activity Budgets

The time budgets for each sample period were calculated as follows:

$$100 \times \Sigma(\text{records for activity i})/\Sigma(\text{records for all activities})$$

With activity i= feeding, travelling, resting or singing. Records from all age-sex categories were pooled together and calculated to produce an overall time budget for the group based on month, season or year, or two years together. I calculated diurnal activity patterns by classifying each sample into each daytime hour interval (*i.e.* combining consecutive 10 minutes samples from each hour) and then using the above formula to calculate the percentage of time spent in each activity for each hour of the day. I also calculated the time budget separately for animal categories: adult male, adult female, subadult and juvenile. Since infants are usually dependent, they have not been dealt with.

The time budget data were based on observation of group B for both 1997 and 1998. Data are also available from some other groups, such as F, G, SCH1, X, but these data not presented here, since the data set is incomplete. No data are available for Group B in November1997, since it was impossible to locate and observe. **Figure 5-1** shows the distribution of activity records for group B by month. **Figure 5-2)** shows the distribution of records by hour of day (pooled across all months). Most data were collected in late dry season and early wet season, from March to June.

5.3. Activity Patterns

5.3.1. General Description

The group usually began to be active around dawn, or a little bit earlier in some days (like 10 to 20 minutes before the dawn). The gibbons become active each day after it is light enough to see. Unfortunately we have very few days which we can confidently know that the group is just leaving the sleeping trees. As mentioned above, based on all day follows, we calculated that the activity period of group B averaged 513±92.6 minutes (n=35).

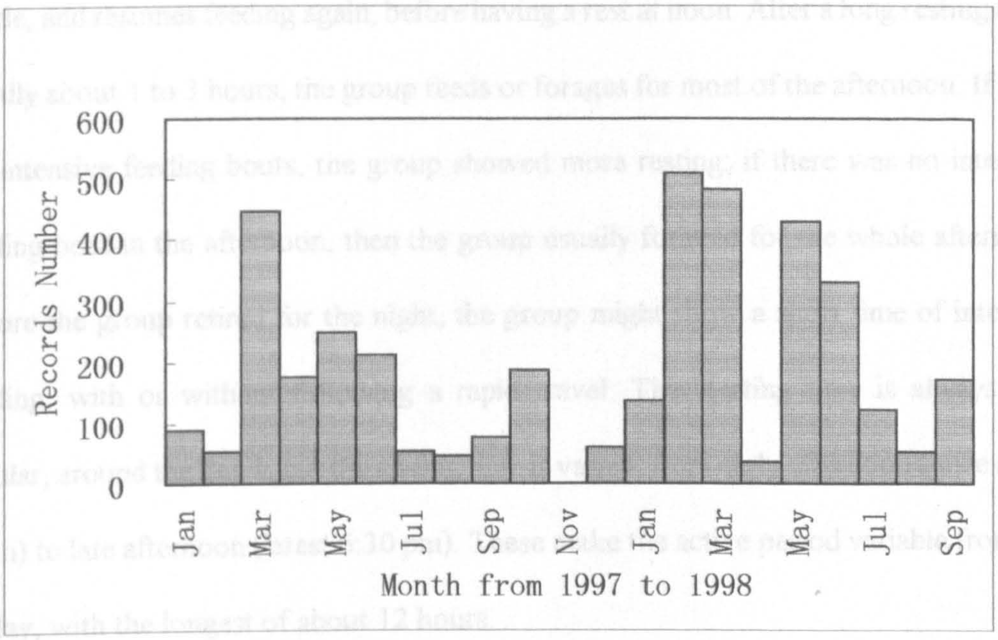


Figure 5-1. The records distribution among different month from 1997 to 1998.

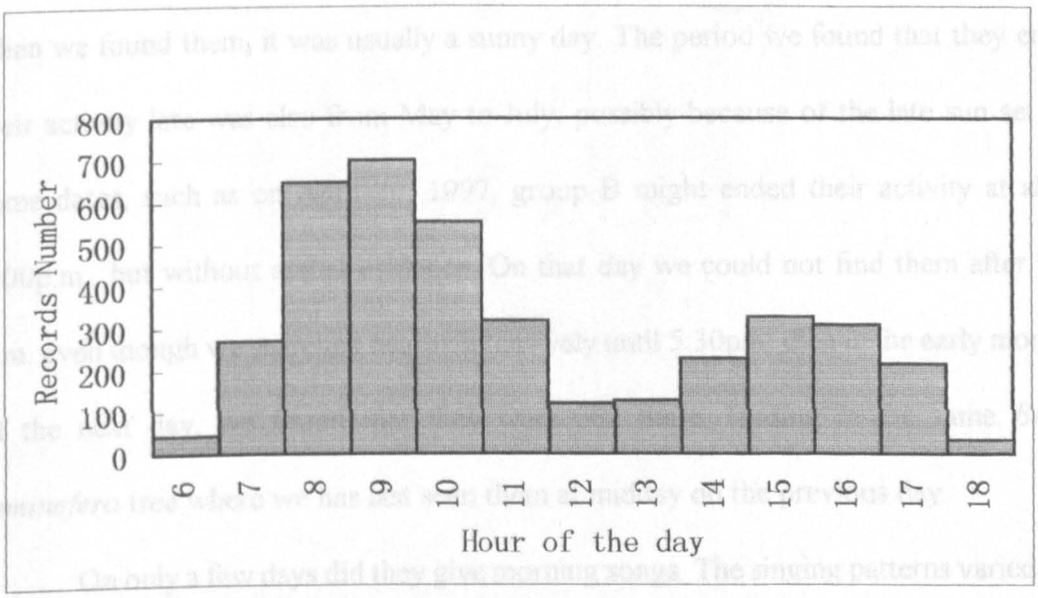


Figure 5-2. The records distribution among daily hour during the two year study period

During or after dawn, group B might go directly on to having morning duets or chorus, or first feed and travel, and then call when at rest. Then the group usually moves a little, and resumes feeding again, before having a rest at noon. After a long resting bout, usually about 1 to 3 hours, the group feeds or forages for most of the afternoon. If there are intensive feeding bouts, the group showed more resting; if there was no intensive feeding bout in the afternoon, then the group usually foraged for the whole afternoon. Before the group retired for the night, the group might show a short time of intensive feeding, with or without following a rapid travel. The starting time is always very regular, around the dawn, but the ending time is varied, from early afternoon (once about 1 pm) to late afternoon (latest 6:30 pm). These make the active period variable from day to day, with the longest of about 12 hours.

The earliest dawning comes in late June, and the earliest mornings are during late May and early June. Late June is usually very rainy; it is difficult to find the gibbons, and rain may delay their activity a lot (Lan, 1989). In those days of late May and early June, when we found them, it was usually a sunny day. The period we found that they ended their activity late was also from May to July, possibly because of the late sun set. On some dates, such as on April 30, 1997, group B might ended their activity at about 1:00p.m., but without actual evidence. On that day we could not find them after 1:00 p.m. even though we searched nearby intensively until 5:30pm; then in the early morning of the next day, we found that they were still there, feeding in the same *Betula luminefera* tree where we has last seen them at midday on the previous day.

On only a few days did they give morning songs. The singing patterns varied with seasons and climatic conditions, as well as with whether other gibbon groups called. In the early morning, they have a major feeding time, either after calling or before going on the next activities (usually rest). They showed some differences between winter and summer time, but variation from day to day is considerable, so the pattern is not rigid as previous studies suggested.

These activities cannot be easily marked out as bouts one by one, but are overlapped or inserted with each other. When singing, there is travelling; when resting, there is playing and other social activity. But some activity, especially feeding, intensive travelling, singing, resting can be recognised as distinct in most situation. The activity cycle is commonly 'rest-feed-rest-feed", with travelling sometimes intensified before or after feeding (resting), or sometimes scattered in feeding bouts (together termed 'foraging').

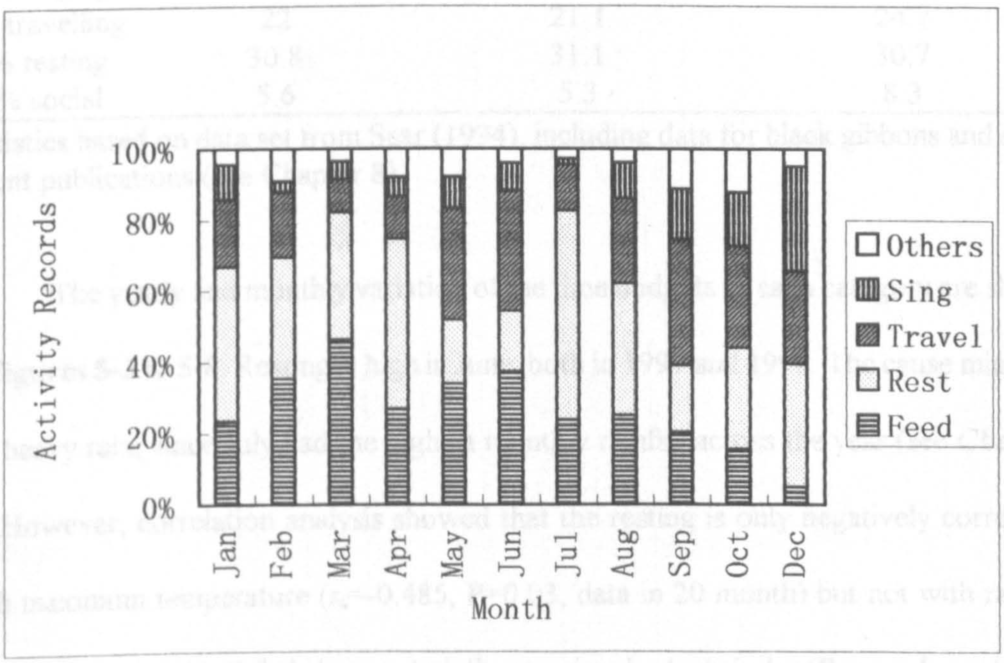


Figure 5-3. The time budget for the group B in different month

5.3.2. Time Budget and Monthly Variation

The time budgets for group B from 1997 to 1998 are shown in **Table 5-1.** In the present study, the budgets for each category are within the range of variation of both all hylobatids and of all black gibbons, although with some small differences. Compared with other gibbons, feeding in black gibbons seems to be low in proportion, with travelling and social time high. Singing, either for present study or for all black gibbons studies, is possibly biased upwards. The reason for this might be explained by the difficulties of observation: when the days gibbons give more calls, we have more observation records. Calls help us to find them (Jiang *et al.*, 1994a; Sheeran, 1993).

Table 5-1. Time budget for present study and its comparison with statistics for hylobatid and black gibbon studies*

Variable	Present Study	*Hylobates* (without *H. concolor*)	*H.concolor* (without present study)
% feeding	34	43.3	29.3
% singing	7.6	4.2	7
% travelling	22	21.1	24.7
% resting	30.8	31.1	30.7
% social	5.6	5.3	8.3

Statistics based on data set from Sear (1994), including data for black gibbons and some recent publications (see Chapter 8).

The yearly and monthly variation of the time budgets of each category are shown in **Figures 5-3** to **5-8**. Resting is high in June, both in 1997 and 1998. The cause might be the heavy rain, since July had the highest monthly rainfall across the year (see **Chapter 4**). However, correlation analysis showed that the resting is only negatively correlated with maximum temperature (r_s=-0.485, P=0.03, data in 20 month) but not with rainfall (r_s=0.047, P=0.845). Rain is known to influence time budgets in *lar* (Raemaekers, 1980). For other activities, the variation is not very clear, although the trend for the same seasons still exist. From March to June, the feeding is higher than in other months. Resting is low in May and June. Travelling is low in March and April.

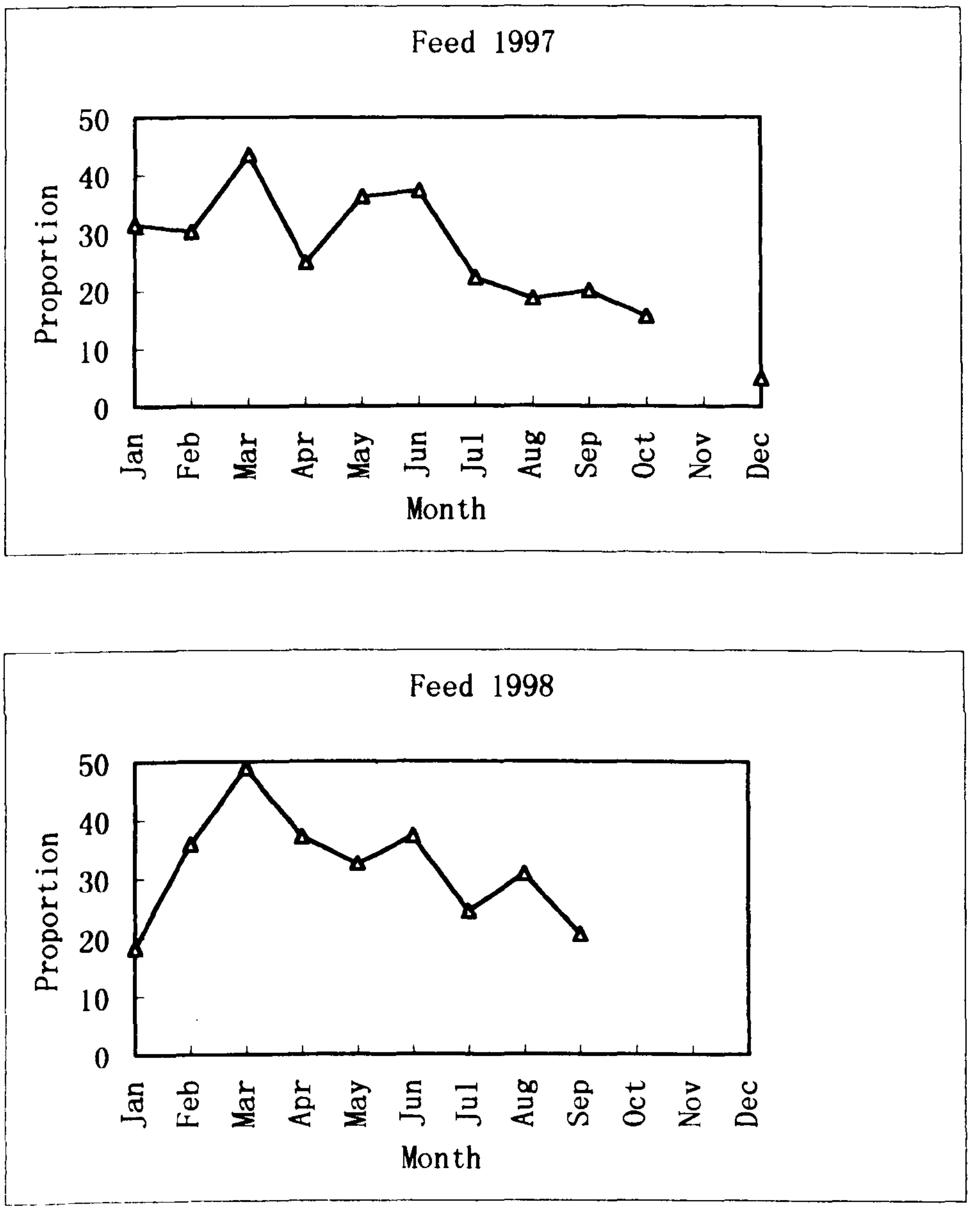
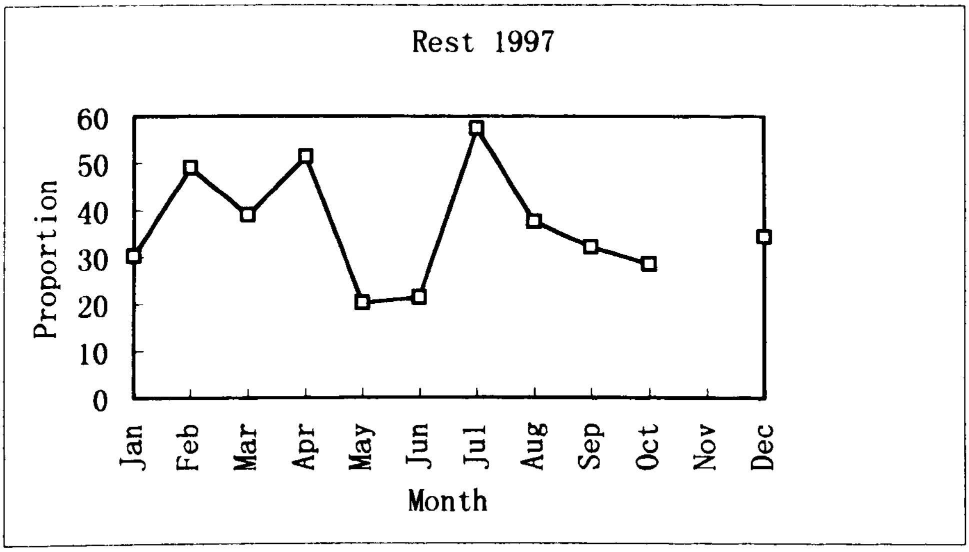


Figure 5-4. Time spent feeding in each month during the two study years.



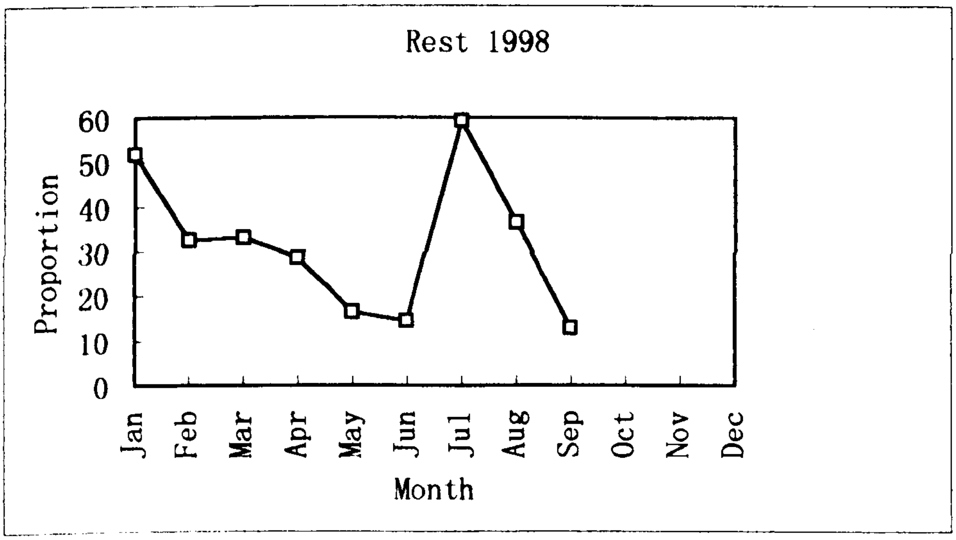
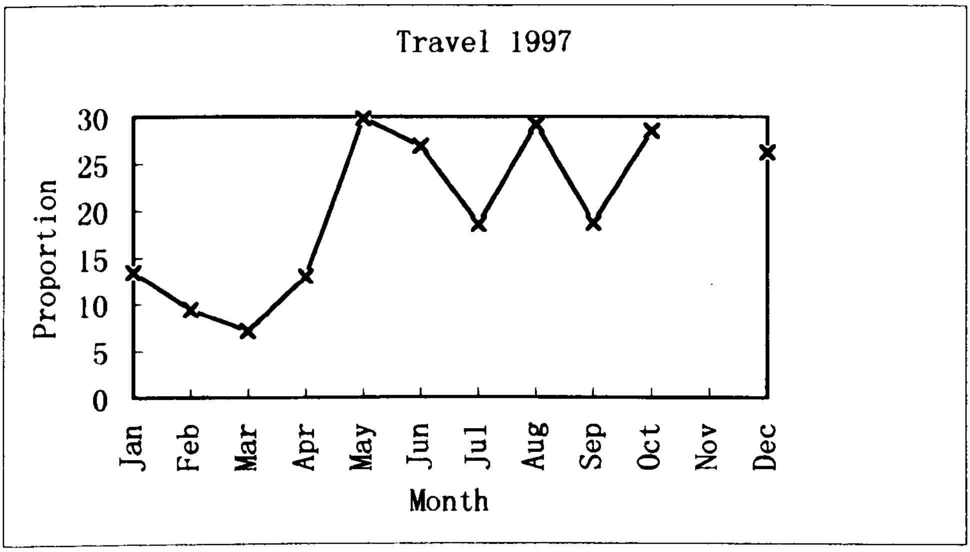


Figure 5-5. Time spent resting in each month during the two study years.



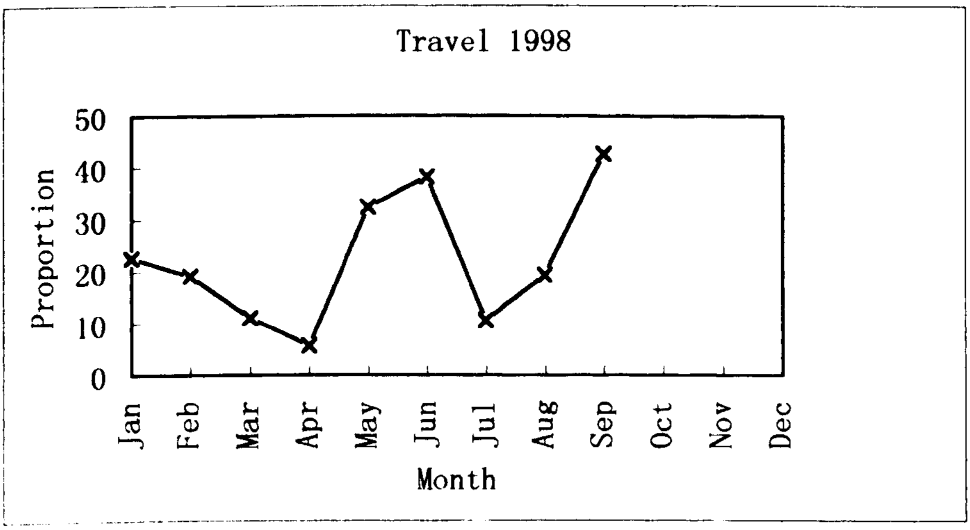
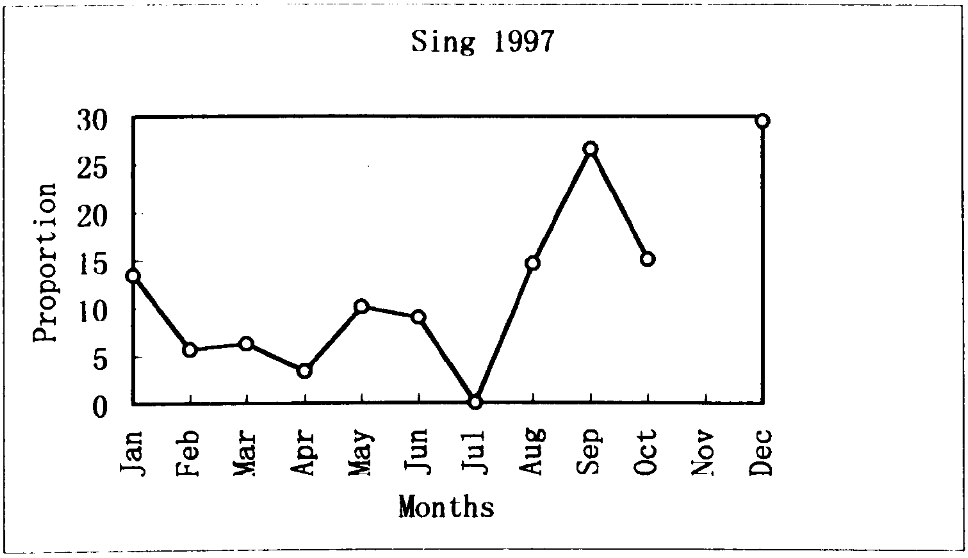


Figure 5-6. Time spent travelling in each month for the two study years.



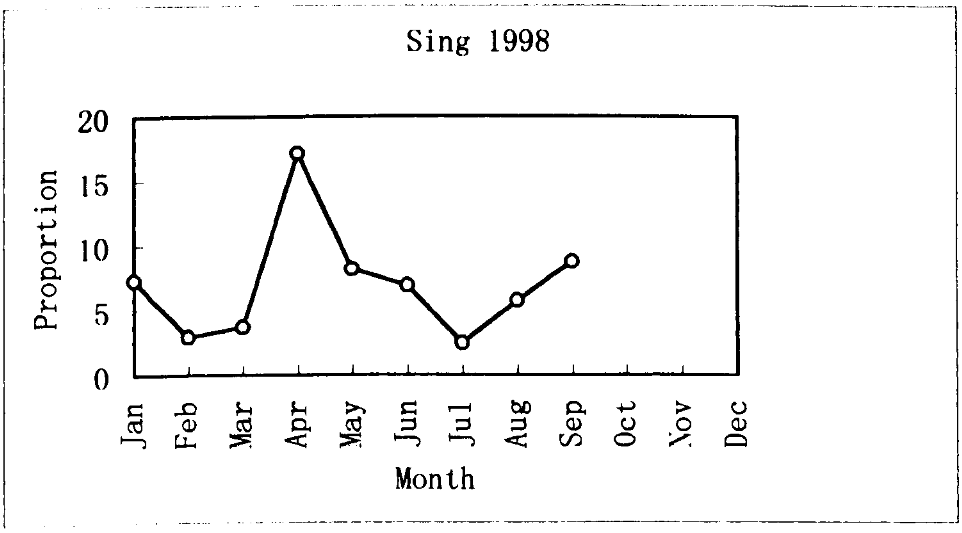


Figure 5-7. Time spent singing in each month for the two study years.

We can rank the food availability by fruit, young leaves and flowers for 4 months from March to June in 1998, the period with the lowest to highest fruit supply (**Figure 4-9**), and the results are shown in **Table 5-2** and **5-3**. Although ripe fruit are in shortage (**Figure 4-10**), young leaves are abundant (**Figure 4-11**), especially in April and May. Flower supply trend (**Figure 4-12**) is similar to the fruit supply in the first two months and to the supply of leaves in last two months. Similarly we ranked the time budget for each activity category (based on **Figure 5-4** to **5-6**) and feeding on fruits, leaves and flowers (based on **Figure 6-4** in **Chapter 6**), for the same 4 months. The results also showed in **Table 5-2**.

Table 5-2. The activity intensity ranks and food availability abundance ranks of group B in 4 months in 1998*.

Category	March	April	May	June
Food availability				
Fruit	2	1	3	4
Young leaves	2	4	3	1
Flowers	1.5	1.5	4	3
Activity				
Feed	4	3	1	2
Rest	4	3	2	1
Travel	2	1	3	4
Feeding[a]				
Fruit	2	1	4	3
Leaves	4	3	1	2
Flowers	3	4	1	2

* a. Feeding intensity is measured by the number of feeding records on each food type (**Chapter 6**).

From **Table 5-2**, we can roughly see that the group rests more and travels less when fruits are not so abundant (but leaves are abundant at these times and the gibbons do feed on more young leaves), while they travel more when they feed more on fruits. Feeding time proportion is significantly related to time spent feeding on leaves ($r_s=1$, $n=4$, $P=0.06$) but not food availability (like fruit), and travelling is significantly related to fruit availability ($r_s=1$, $n=4$, $P=0.06$) but not with how much fruit they feed on. These reveal that feeding time is not determined by fruit availability, but depends on food quantity fed on, while travelling is determined by how much fruit availability the habitat provides. Furthermore, if we compare the three periods with more sample records (February to March, May to June, and September to October), we can see that feeding is related directly to the abundance of *ripe* fruits ($r_s=1$, $n=3$, $P=0$), but travel (with ripe fruit: $r_s=0.55$, n=3, P=0.667) and rest (with ripe fruit: $r_s=-0.55$, n=3, P=0.667) may also be related to other factors (**Table 5-3**). Resting time is high in seasons with less fruit but abundant young leaves (usually patchily distributed). When fruit is available and abundant, and the gibbons feed more on fruits, and rest time becomes low. Travelling time is high when fruit is abundant, perhaps because the gibbons spend time looking for fruits; but travelling is the lowest in season without fruits.

Table 5-3. The activity intensity ranks and food availability abundance ranks of group B for some seasons from 1997 to 1998.

Season	Ripe fruit availability	Feeding	Resting	Travelling	I_δ
Feb-Mar	Low	Low	High	Low	2.43
May-Jun	Middle	Middle	Low	High	2.42
Sept-Oct	High	High	Middle	Middle	1.36

I_δ is Morisita Index, show the distribution pattern of the home range use (**Chapter 7**).

The trend in seasonal variation among activities is not clear. But if all data are lumped together for the different seasons, the time budget for the wet season and dry season exhibit some differences (**Figures 5-8** and **5-9**). Both feeding and resting decrease during the wet season, but travelling, singing, and other social activities increase, but only travelling showed significant differences (t=-2.727, P=0.017, each season in 10 month data). Bias is possible, since during the wet season few data are available. In the wet season, only obvious activities such as travelling and singing are easily detected; the others (such as feeding and resting in the dense tree leaves) are difficult to see. It seems nothing can be done about this problems at present.

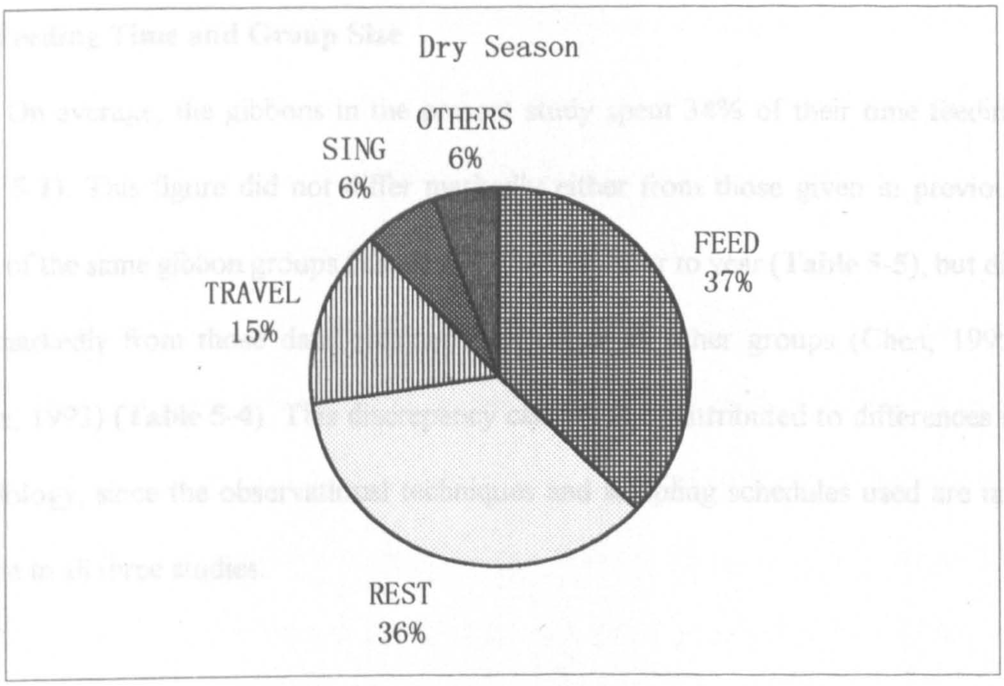


Figure 5-8. The time budget for the dry season (10 months in two years)

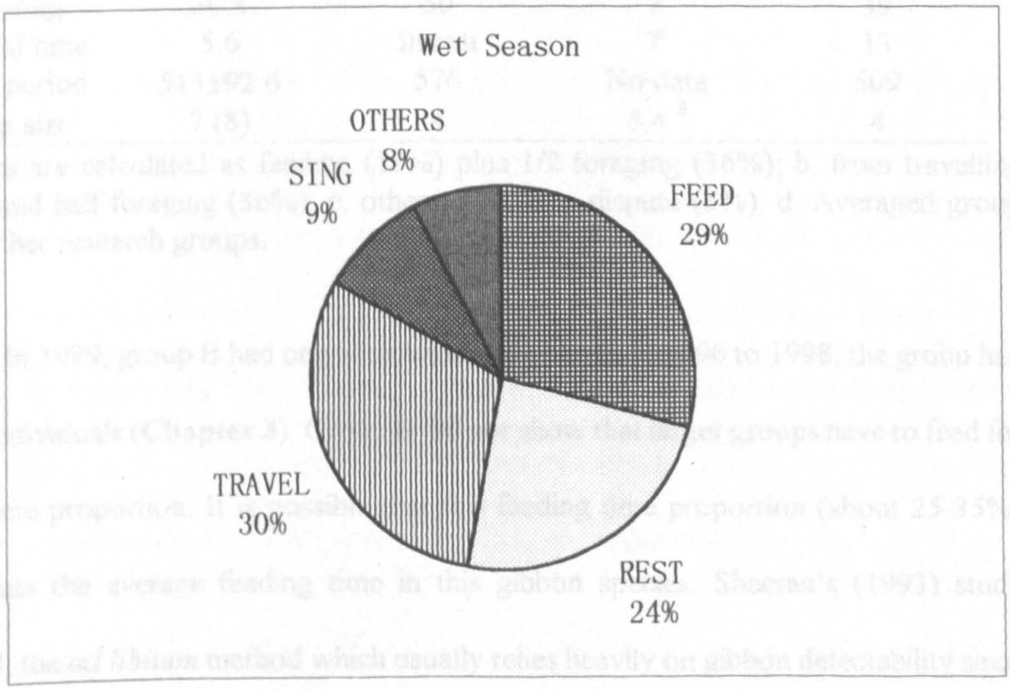


Figure 5-9. The time budget for group B in wet season (10 months in two years).

5.4. Activity and Group Size

5.4.1. Feeding Time and Group Size

On average, the gibbons in the present study spent 34% of their time feeding (**Table 5-1**). This figure did not differ markedly either from those given in previous studies of the same gibbon groups (**Table 5-4**), or from year to year (**Table 5-5**), but did differ markedly from those data obtained by studies on other groups (Chen, 1995; Sheeran, 1993) (**Table 5-4**). This discrepancy can be partly attributed to differences in methodology, since the observational techniques and sampling schedules used are not the same in all three studies.

Table 5-4. Comparison of activity budgets for the four studies*.

Variable	Present Study	Lan (1989)	Sheeran (1993)	Chen (1995)
% feeding	34.0	33	36[a]	19
% singing	7.6	3	17	1
% travelling	22.0	14	32[b]	28
% resting	30.8	50	8	39
% social time	5.6	In rest	7[c]	13
Active period	513±92.6	576	No data	509
Group size	7 (8)	4	5.4 [d]	4

*a. Data are calculated as feeding (18%) plus 1/2 foraging (36%); b. from travelling (14%) and half foraging (36%); c. others (4%) plus dispute (3%). d. Averaged group size for her research groups.

In 1989, group B had only 4 individuals, whereas in 1996 to 1998, the group had 8 or 7 individuals (**Chapter 3**). Group B did not show that larger groups have to feed for more time proportion. It is possible that this feeding time proportion (about 25-35%) represents the average feeding time in this gibbon species. Sheeran's (1993) study showed, the *ad libitum* method which usually relies heavily on gibbon detectability since the animals are not habituated, would result high frequencies of travelling and singing, but low resting time. In her data, feeding is a little bit higher than the average for black gibbons, and still lower than all hylobatids. For Chen's (1995) study, feeding (19%) is too low (the lowest in all studies, except John's (1986) disturbed population in selective logging habitat), and travelling (28%) is high, if compared with all hylobatid data (**Table 5-1**). However, all these data are within the range shown by hylobatids. So from this point of view, the feeding proportion in present study is typical.

The time budget data from present study also differ from that of my previous study (Lan, 1989): more travelling and singing, less resting (**Table 5-2**). My previous study was likely to have suffered from serious seasonal influences because the observations for the year 1989 were concentrated in February and March (in the middle of the dry season). In this season, group B spent a larger proportion time feeding on leaves (abundant food resources) on the deciduous tree *Betula luminifera*. If we just compare the time budget for this season (**Table 5-6**), the feeding proportions for 1997 and 1998 were higher, and resting were lower than that of 1989. If the differences are not yearly variation, the different methodology used should be the cause, since in 3 periods, the data are in general abundant owing to good observation condition. In my previous study (1989), the data were from 5 all-day follows, and part-day follows were excluded from the calculation. Non-obvious activity under the tree canopy was categorised as rest, so were social activities such as playing and grooming which is usually common in the morning sunning resting bout. In contrast, for 1997 to 1998, data from part-day follows were included in the analysis: this possibly increases the active categories, but not those difficult-to-detect activities such as rest when under the canopy.

Table 5-5. Comparison of activity budgets for the two studies on group B (1989 and 1997-1998)*.

Variable	1989	1997[a]	1998[b]	1997-98
% feeding	33	32.5	35	34
% singing	3	9.3	6.3	7.6
% travelling	14	18.5	24.4	22
% resting	50	33.9	28.7	30.8
% social time	Lumped in rest	5.7	5.5	5.6
Group size	4	7	7	7

* a. Time from January to October 1997 (10 months), not including data of December 1997,and no data for November 1997. b. From December 1997 to September 1998 (10 months).

Table 5-6. Comparison of activity budgets for the two studies on group B in the same months (February and March) both 1989 and 1997-1998.

Variable	1989	1997	1998	1997-98
% feeding	33	42.1	42.3	42.2
% singing	3	6.2	3.3	4.3
% travelling	14	7.4	15.3	12.6
% resting	50	40.1	32.7	35.2
% social time	lumped in rest	4.2	6.4	5.7

February and March are in the middle of the dry season: the temperature is still low but going up, and the diet quality is bad (mainly young leaves)and quantity low (usually the worst season for fruit, flowers and young leaves). The black gibbons might adopt a strategy of increased feeding and resting, but reduced travelling time to deal with the energy stress. Feeding can increase the quantity of food ingested, and resting can reduce energy consumption. (Travelling is the most energetically expensive activity).

When the time budget data are divided by months there is no significant relationship between feeding and travelling (Spearman's rank correlation: r_s=-0.245 , n=20 monthly samples, P=0.298), between feeding and resting (r_s=-0.284, n=20, P=0.225) or between feeding and other activities. However, when the 1997 data are analysed by hour of day, feeding is positively correlated with travelling (Spearman's rank correlation, r_s=0.7025, n=13, P=0.007), and the resting is not correlated with feeding (Spearman rank correlation, r_s=-0.3329; n=13, P=0.226).

5.4.2. Travelling and Resting

We can explain the variation in the amount of time spent travelling based on differences in group size in both studies of the same group: the larger group will tend to deplete resource patches faster than the smaller group, so they will be forced to visit more patches in order to satisfy the group's requirements. Consequently, more time must be spent travelling and energetic travel costs are increased. This in turn further increases the metabolic requirements of the group, thus compounding the effect of increased group size. It would therefore be expected that the smaller Xiaobahe group would spend substantially less time travelling in 1989 than in 1997-1998. In fact, group B did spend more time travelling when the group became larger in some years (**Table 5-4** and **Table 5-5**). As yearly variation existed, such as that the travelling time in 1997 is lower than that in other years (**Table 5-5**), so the group size is not the best explanation. It is possible that during February and March, the groups have a lot of young leaves to eat, so the time for travelling reduced even though group size is bigger. When the gibbons have more leaf in the diet, then time spent travelling should decrease. In contrast, when the fruit are a relatively more important part of diet, *i.e.* during the wet season, the travelling proportion will be higher, too, because looking for fruit are more time-consuming than feeding on leaves, and this is the case in present study (**Figure 5-8** *vs.* **Figure 5-9**).

In this study, resting and travelling are inversely significantly correlated (r_s=-0.589, n=20, P=0.006). When gibbons have to travel more, they have to feed more, and then they have no spare time to rest. Only when they have a surplus of high quality food, or abundant and easily accessible food, something like abundant young *Betula liminifera* leaves during February and March, do they have more time free that can be devoted to rest. In winter and early morning when the temperature is low, group B (other groups as well) usually have a long time sun-bath, either during resting or feeding bouts, or both. Resting is energy-saving, and sun-bathing is for energy saving and acquiring. This might explain why the group B showed a high rest in middle to late dry season from January to April (July is different because of heavy rain, see above discussion), and the difference between dry and wet seasons (**Figures 5-8** *vs*. **5-9**). In other seasons with enough energy surplus, when feeding is increased, the time for rest could have been used for feeding and travelling when necessary.

Resting is negatively correlated with singing (r_s=-0.552, n=20, P=0.012). It is not very difficult to explain the relationship of resting with singing. High resting means high young leaf abundance (as mentioned above), and they do not need to advertise their status as singing is an index of competition intensity, and saving energy like calling is energy expensive.

An alternative explanation is that travelling costs do not, in fact, increase in direct proportion to group size. Feeding effort and travelling effort might not increase in large group so long as the size of the group does not exceed the capacity of the resource patches it feeds on. But this explanation requires more evidence and discussion (see **Chapter 9** for more discussion).

As expected, given the increase of the group size, and the less time spent travelling, time spent resting is higher in the previous study (1989) than the present one (1997-1998). This supports Dunbar and Sharman's (1984) argument that resting time acts as a reserve of 'spare' time that can be drawn on for other activities.

5.4.3. Singing and Socialising

The other time budget components, singing and socialising (grooming, scanning, playing), tend to occupy a constant low proportion of the time budget (less than 20% in each month except September to December: **Figure 5-4**). As might be expected, given the decrease in activity categories, such as travelling and feeding and the increase in other categories like resting, time spent in social behaviour should be high, since social activity is usually connected to rest time. But in this study, the trends are not clear. Although singing and socialising activity go up between September and December in 1997 (**Figure 5-5**, no data in 1998), the small sample size might be responsible (for records data, see **Figure 5-1**). Compared with the previous study (1989), these activities increase in both 1997 and 1998, suggesting that group size may be an important factor. There are more infants and juveniles in the recent study, but not in earlier periods. The juvenile and subadult were of similar ages in group during the study period (less than one year apart: see **Chapter 3**), and they really showed a lot of play. Singing might be biased by the data-collection method, since the singing data from 1989 are based on several days with whole day following, but the data for 1997-1998 study include data from incomplete days.

As mentioned before, the differences between various studies (**Table 5-2**) might reflect the methods used. The data collecting method used by Sheeran is *ad. libitum*, so singing and social time are high (in contrast resting time goes down rapidly). With *ad. libitum* methods, rest time will usually be low since detectability is poor when the gibbons are at rest. Chen's (1995) result is similar to my previous study (Lan, 1989), and resting and social activity together are high (52%), while singing is low if it is considered only as the morning duet. Of course, his data on feeding and travelling is clearly different from both of my studies (see discussion above).

5.5. Diurnal Activity Variation

Variation in activity throughout the day is shown in **Figures 5-10** to **5-14**. The Xiaobahe gibbon show a fairly typical gibbon pattern, with a peak in feeding at the beginning of the day, a midday rise in resting and social time (with a concomitant reduction in travelling time) followed by another smaller peak in feeding during the late afternoon. Except for the decrease in singing (usually high in the early morning), feeding is intensive in the early morning, then they rest in late morning, and then feed and travel again in the afternoon. Both feeding and travelling together is defined as 'foraging' in other studies (Gittins, 1982), so the main activity in the afternoon is foraging. In general, travelling is quite evenly distributed throughout the day time. Social activity usually occurred after the early morning feeding period, mainly in the late morning and noon. Grooming and scanning typically occur in late morning, but play at noon.

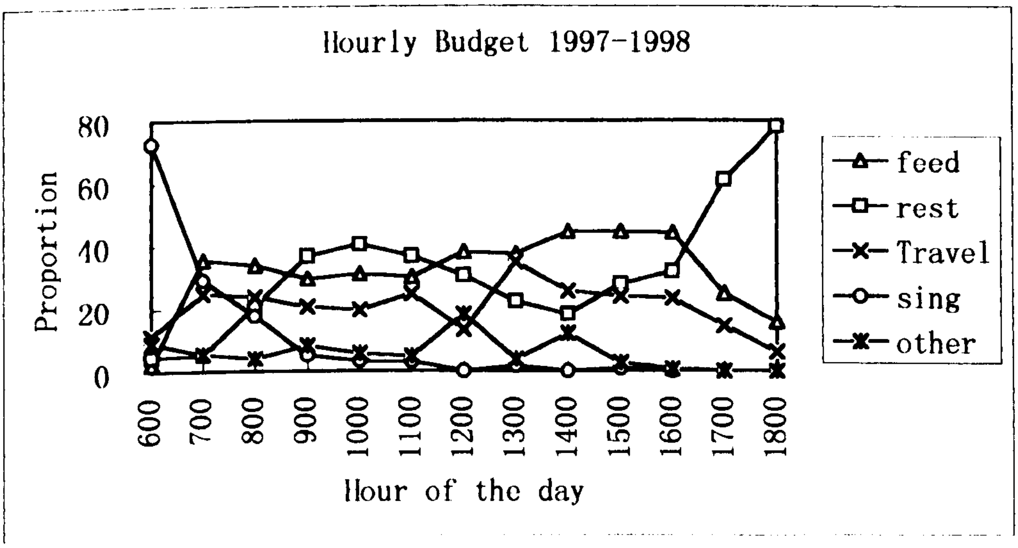
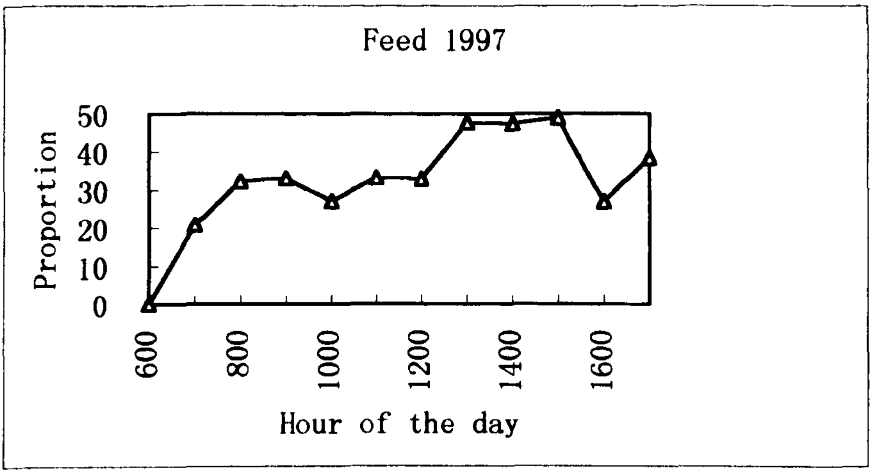


Figure 5-10. The time budget among daily hours during the two study years.

Chen (1995) has given a clear indication about changes in activity patterns across day time. Although some points such as that travelling time were evenly distributed over the day, and singing, grooming and play (together categorised as "other activity" in my study) showed a similar trend, the present study is quite different from Chen's result. The main difference is in resting and feeding. In Chen's study, resting is high in the afternoon, and feeding is high in the morning. In present study at Xiaobahe, resting is high in the morning, feeding is quite evenly distributed across the day, with foraging being more intensive in the afternoon.

Records distribution differences between the two studies might have effects for the difference between the two studies. Data from the present study are centred in the morning, and Chen's observations were made more in the afternoon, and mainly in middle to late dry season. If gibbons rest more in the afternoon (and usually under the canopy in the dense leaves), it could be very difficult to observe them. Seasonal differences in the number of records centring between the two studies might also have effects for the difference between these two studies. Chen's records were mainly limited to a few months including wet months, from May to June, whereas most of our data were collected in dry season. Unique time showed a unique feature, as our data show that the activity patterns may change from year to year, as the data for 1997 and 1998 are different (although small sample size might be a source of bias).



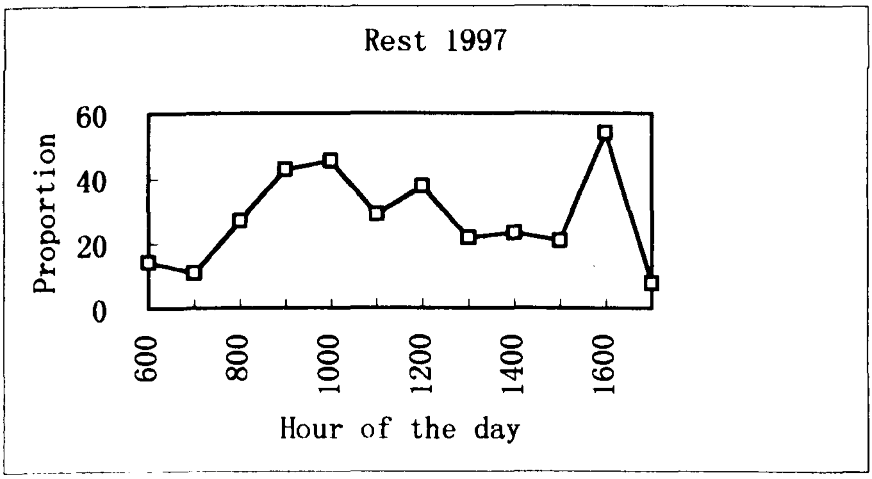
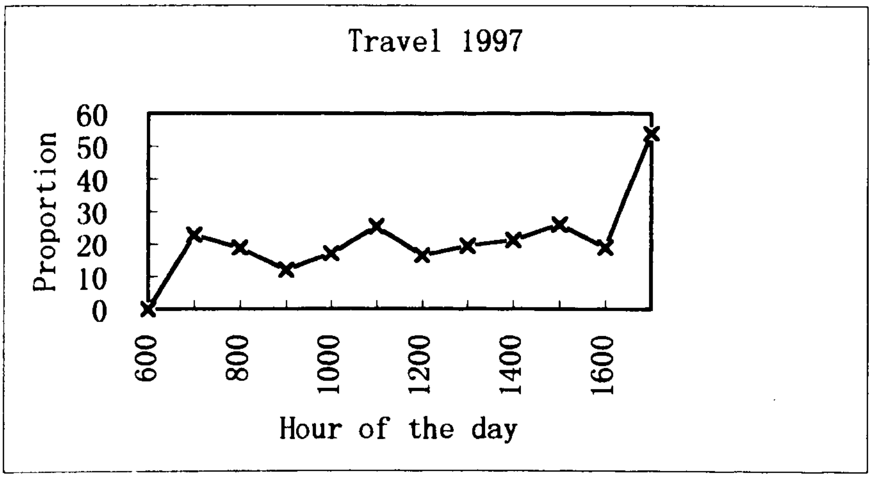


Figure 5-11. The time budget variation among day time in 1997.



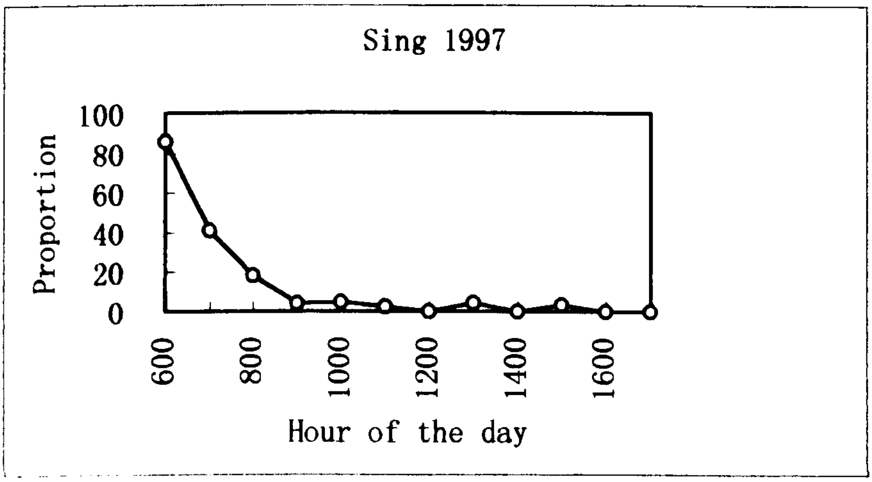
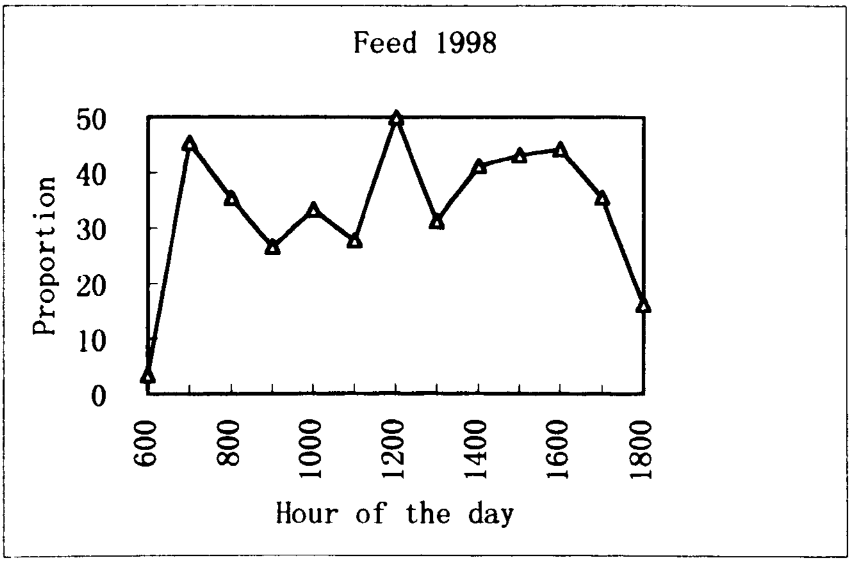


Figure 5-11. The time budget variation among day time in 1997.



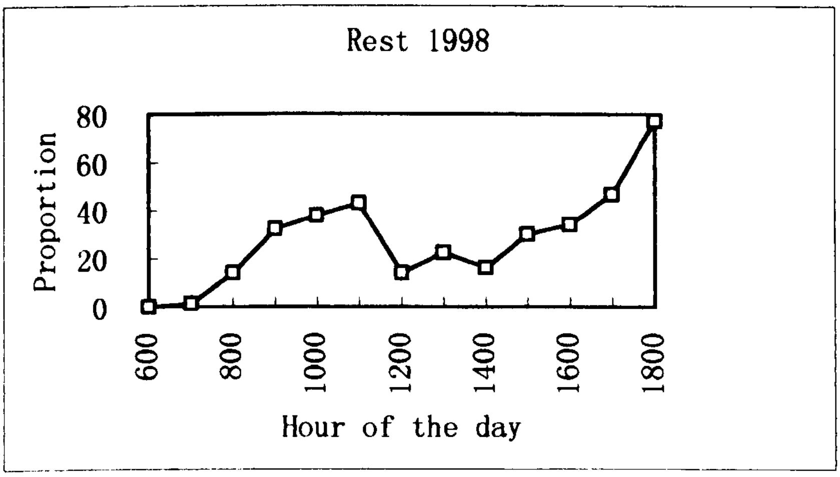
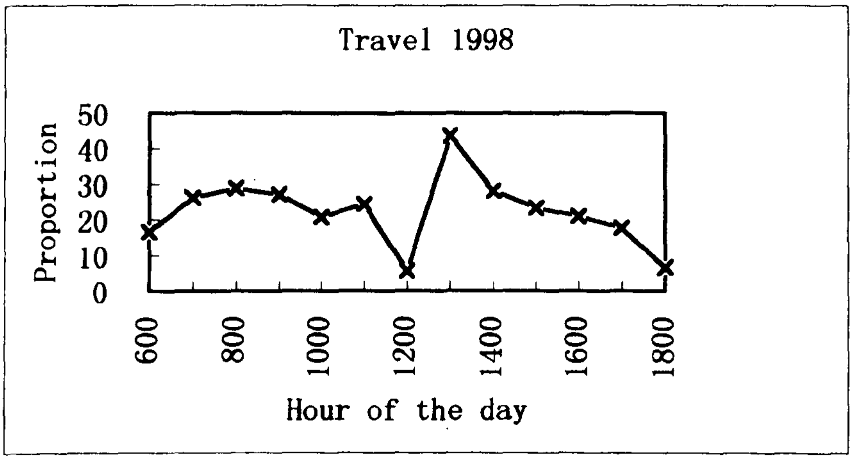


Figure 5-12. The time budget across the day time in 1998



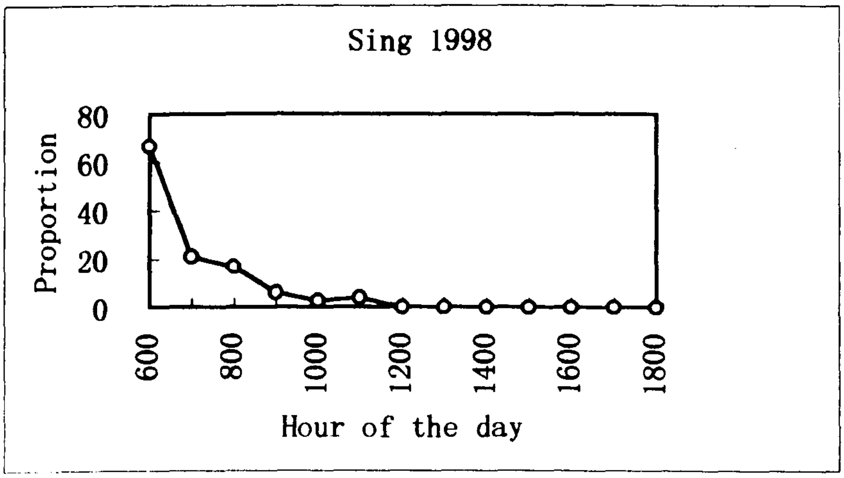


Figure 5-12. The time budget across the day time in 1998

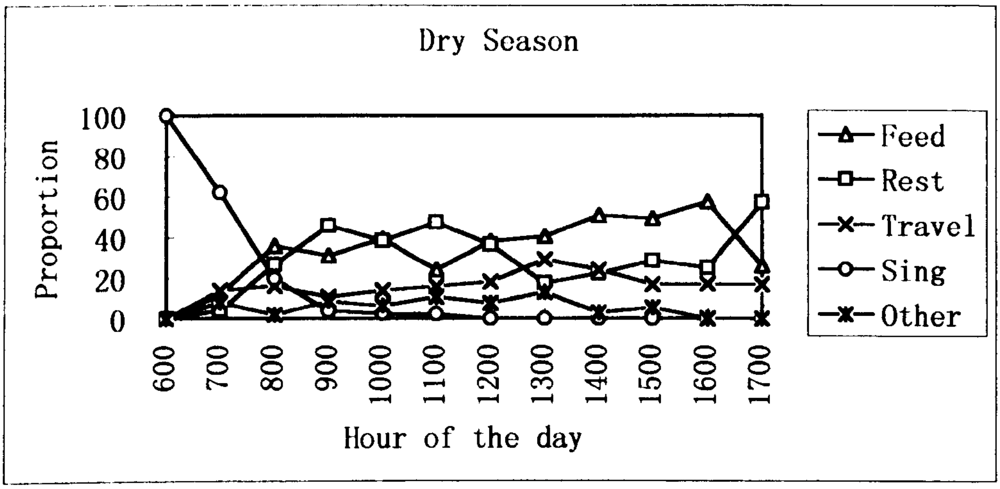


Figure 5-13. The activity variation across day time during dry season for the two years combined.

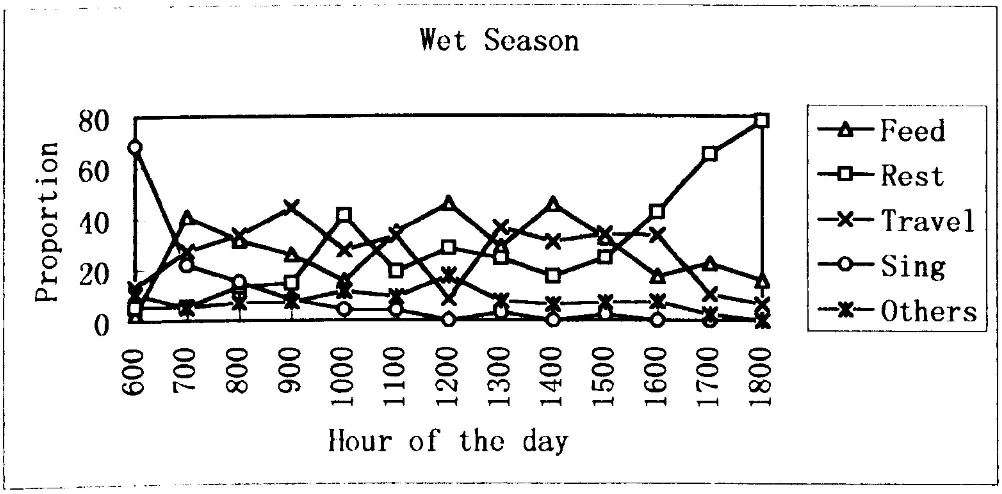


Figure 5-14. Activity variation across the day during wet season in the two study years for group B.

The similarity of present study to the other gibbon daily activity patterns can be explained as follows. An early morning feeding peak possibly serves to replenish energy stores depleted overnight. High levels of resting during the late morning in the wet season, and mid to late morning in the dry season could be a response to low temperature, but the high level of resting at noon in Chen's (1995) research group may be a response to high temperature.

A comparison of daily activity patterns between years, seasons ('wet' if monthly rainfall more than 100 mm; and 'dry' if monthly rain less than 100mm) and different sites or groups reveals that there was pronounced variation. It thus seems likely that activity was influenced by many factors, such as heavy rainfall. The fact that there is no definite resting peak in the afternoon implies that midday and afternoon temperatures did not inhibit the black gibbon's activities as happens in other conspecifics in more southern range areas. The temperature usually is not high at all for black gibbons, if compared to the habitats of other gibbon species (**Chapter 4**).

5.6. The Time Budget Difference Between Age-sex Classes

The time budgets of the different age-sex classes exhibit some differences. The adult female and adult male show similar proportions of most activities, but those for the juvenile and subadult are of different proportion, especially for singing (female-juvenile: t=4.85, n=19, P=0; male- juvenile: t=5.97, n=18, P=0) and travelling (female-juvenile: t=-3.81, n=19, P=0.001) (**Figures 5-15, 17, 18**). Their singing is the least, but travelling, and others activities (like playing) (female-juvenile: t=-6.069, n=19, P=0) are more intensive than adults. They rest less than travel, whereas adults rest and feed in similar proportions and do so more than travelling. Time budget variation across months is shown in **Figures 5-15, 17, 19** for each age-sex class. The correlation between the various age-sex classes are as follows:

Between females and males: feeding is almost significantly correlated (r_s=0.445, P=0.056, n=19 months), resting is very significantly correlated (r_s=0.583, n=19, P=0.009), travelling is of not correlated (r_s=0.268, n=19, P=0.267), singing is significantly correlated (r_s=0.574, n=19, P=0.01).

Between female and the subadult/juvenile, neither feeding (r_s=0.217, n=20, P=0.359), resting (r_s=0.245, n=20, P=0.298), nor singing (r_s=0.265, n=20, P=0.259), are significantly correlated, but travelling is (r_s=0.573, n=20, P=0.008).

Between adult male and subadult/juvenile, no activities are correlated significantly: feeding (r_s=0.398, n=19, P=0.092), resting (r_s=0.054, n=19, P=0.825), travelling (r_s=0.181, n=19, p=0.459) and singing (r_s=0.383, n=19, P=0.106).

For the adult females, resting is inversely correlated with travelling and singing significantly (travelling: r_s=-0.481, n=20, P=0.032; singing: r_s=-0.75, n=20, P=000). For the adult male, resting is negatively correlated with feeding (r_s=-0.485, n=19, P=0.035) with travelling (r_s=-0.059, n=19, P=0.007) and with singing (r_s=-0.607, n=19, P=0.006). For the subadult/juvenile, only resting is correlated with travelling (r_s=-0.594, n=20, P=0.006), and feeding with travelling (r_s=-0.486, n=20, P=0.030). All these can be explained by the fact resting is as a reservoir for other activity as suggested by Dunbar (1988).

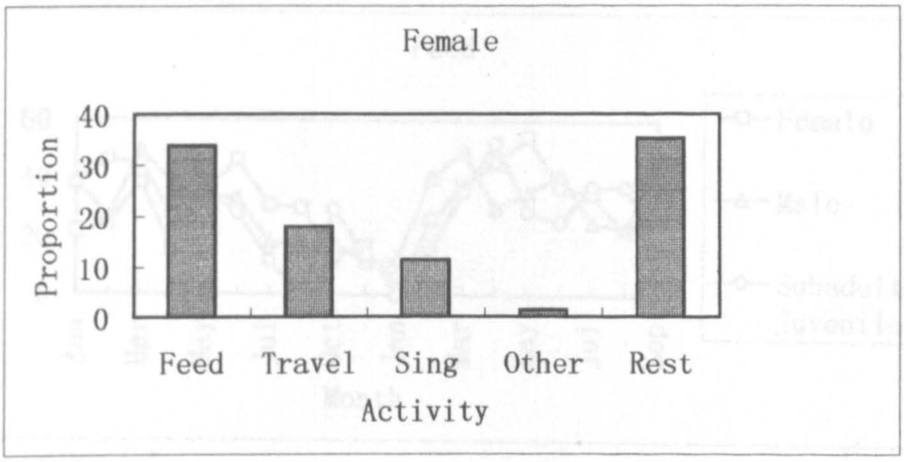


Figure 5-15. The time budget for adult female of group B.

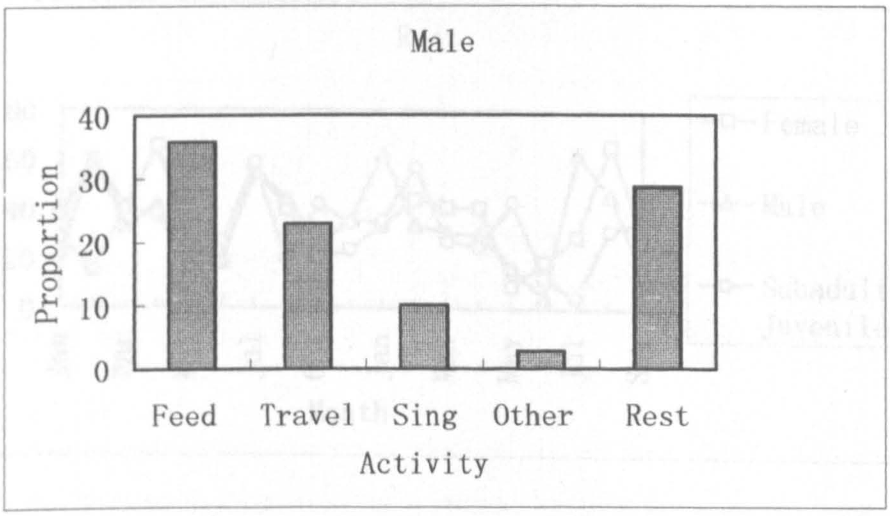


Figure 5-16. Male time budget.

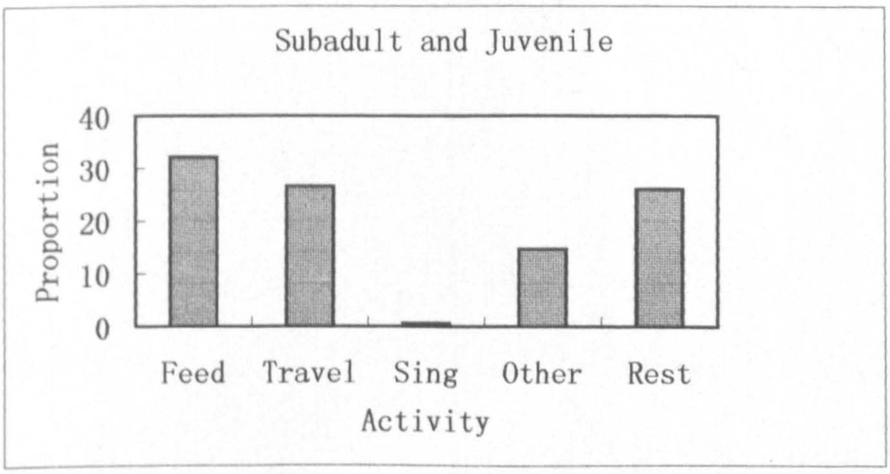
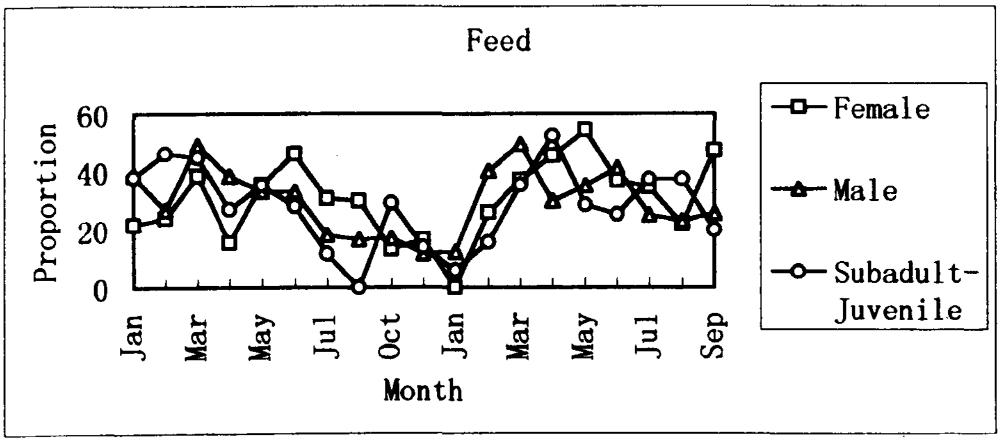


Figure 5-17. The time budget of subadult and juvenile individuals.



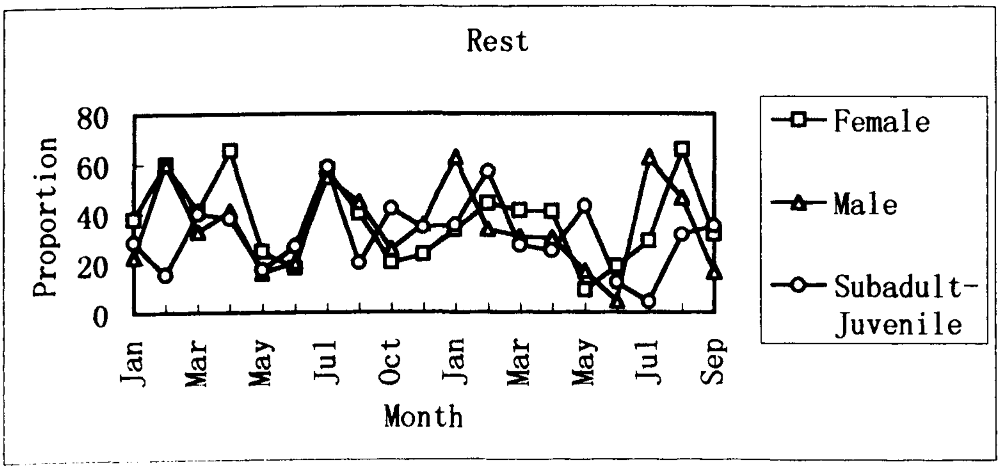
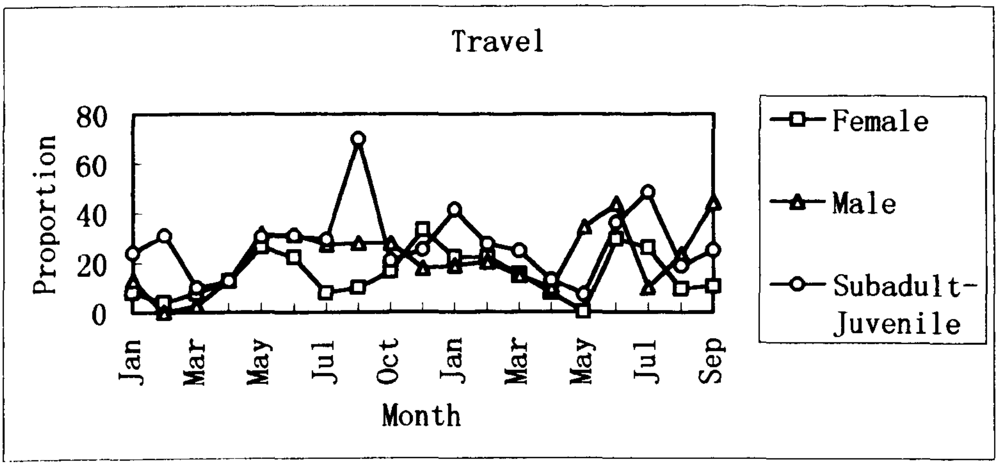


Figure 5-18. The time budget monthly variation of different age-sex group, from feeding, to resting, travelling, and singing.



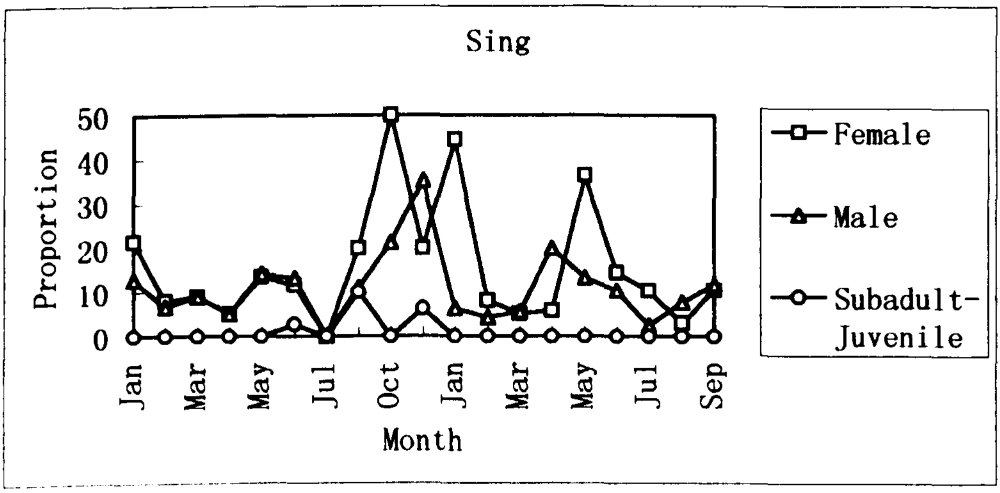


Figure 5-18. The time budget monthly variation of different age-sex group, from feeding, to resting, travelling, and singing.

5.7. Summary

In this chapter I have described the activity patterns and activity budgets for Xiaobahe black gibbons. They are broadly similar to other Hylobates field studies where comparable data are available. The feeding, resting, travelling are the main three activity categories. Singing is one prominent activity in their daily life, usually in the morning, but with low proportion in the total time budget. Other activities, such as grooming, playing are rare and mainly limited to specific age-sex groups (playing in juveniles and infants, grooming mainly in adults), and mainly occurred during the resting period (in the morning, with sun bathing).

Many factors affect the time budget, such as group size, food availability, and the time of day. Seasonal and yearly differences existed. In the wet season, feeding and resting become less, but travelling and singing increase. This might be a response to the abundant fruit availability in this season. Daily differences also exist, although they in general follow a typical gibbon daily activity pattern. Different age-sex groups showed difference in activity, too.

CHAPTER 6. FEEDING BEHAVIOUR

6.1. Introduction

Most gibbons are highly frugivorous, spending between 22% to 89% of their feeding time on fruits (Sear, 1994). Indeed, much of gibbon anatomy, for example long limbs, and light body, is apparently designed for soft fruit ingestion, and for effective foraging in terminal twig patchy fruit resources. This frugivorous diet is supplemented by other food items such as flowers, insects and leaves, particularly at times of low fruit availability. Dietary shift is usually not seen in most gibbon populations, but some populations, *i.e.* hoolock and black gibbons, may be the exception. Dietary shifts usually lead to behavioral repercussions and changes in primate activity budgets (Oates, 1987). In contrast to other gibbons, black gibbons might experience a fission and fusion pattern (Jiang *et al*, 1994c; Liu *et al.*, 1984), similar to spider monkeys. The unstable food availability in the latter's habitat has resulted in its fission-fusion social grouping pattern (Robbins, 1991, Wallace, 1998). Understanding diet and feeding behaviour, as well as resource availability within the habitat, are important to understanding the social organization of black gibbons.

In this chapter, I attempt to characterise the diet and foraging behaviour in relation to the temporal distribution of their food resources. Following a brief review of the methods used to measure certain behavioural and ecological variables (**6.2.**), I go on to describe diet source and fruit type (**6.3.**), plant species (**6.4.**), and feeding time ecology (**6.5.**), diet variation and selectivity (**6.6.**), food tree dominance (**6.7**) and animal foods (**6.8.**) and summary (**6.9**).

The food and feeding behaviour of black gibbons have been studied since my first field trip to study the gibbons in 1987. However, the diet data presented here were collected between January1997 and October 1998. Most feeding data were based on observation of group B. Some data are also available from other groups, such as F, G, SCH1, X. No data are available for Group B in November1997, since it was impossible to locate and observe them. Only a few data are available in December 1997. Most data were collected in late dry season and early wet season, from February or March to June (**Figure 6-1**).

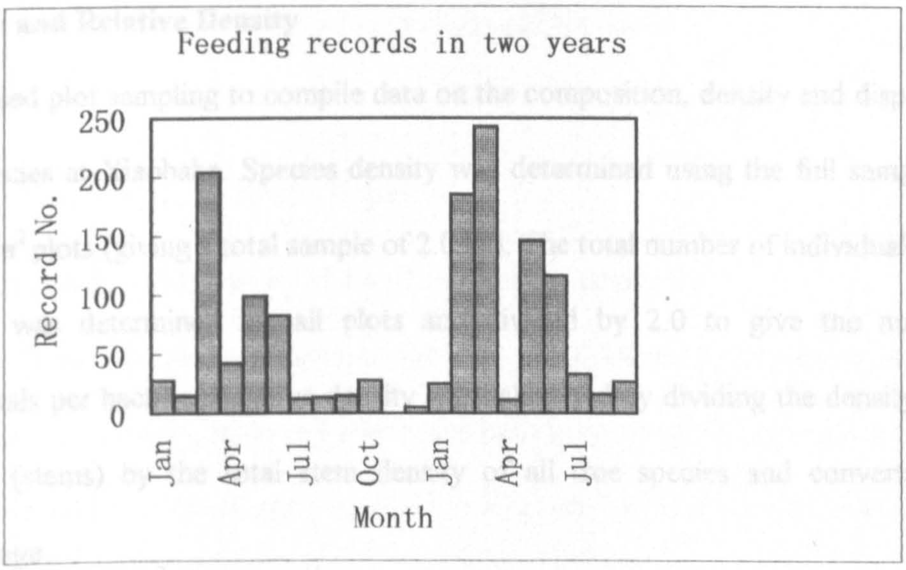


Figure 6-1. The total records for the feeding activity

6.2. Method

6.2.1. Behavioural Measures

Electivity Index

In order to determine species preference for food items, I use Electivity indices. Electivity indices are a variant of the more familiar selection ratios, having the values between -1 and +1 (Barrett, 1995). The calculation is based on the following formula.

$$Ei=(r_i-n_i)/(r_i+n_i)$$

where r_i is the percentage of species i in the diet, and n_i is the relative availability of species i.

When the Ei is -1, that means gibbons eat nothing from the species, when the Ei is 0, that means that the gibbons eat the resource in proportion to its relative availability. When the Ei is more than 0, that means that the gibbons eat more of this species than its relative availability.

6.2.2. Ecological Measures

Density and Relative Density

I used plot sampling to compile data on the composition, density and dispersion of tree species at Xiaobahe. Species density was determined using the full sample of 20 20x50 m^2 plots (giving a total sample of 2.0 ha). The total number of individuals of each species was determined for all plots and divided by 2.0 to give the number of individuals per hactare. Relative density was calculated by dividing the density of each species (stems) by the total stem density of all tree species and converting to a percentage.

Morisita's Index

Species dispersion or patchiness was estimated using Morisita's indices (Barrett, 1995; Poole, 1974). Data were obtained from the same sample of 20 individual 20x50 meter quadrats for group B. Morisita's index, I_δ, provides a measure of the extent to which individuals of a particular species are non-randomly distributed among identically sized quadrats. An index value of 1 indicates a random distribution, while those less than or greater than 1 indicate uniform and patchy distribution respectively. I here take the conservative index value of 2 or more to indicate patchiness, while those species with values less than 2 were considered to be uniformly distributed. Morisita's index is calculated as follows:

$$I_\sigma=\Sigma(n_i(n_i-1))/(n(n-1)) \times N$$

when N is the number of quadrats in which a species found, n_i is the number of individuals of the species in the *i*th quadrat, and n is the total number of individuals of a species in all quadrats. Since Morisita's index should only be used when there are 10 or more individuals of a species, another simpler measure of dispersion was also used. Species were designated as patchy if there were less than 5 individuals per hectare, and uniform if there were more than 15 individuals per hectare.

6.3. Diet Source and Fruit Types

6.3.1.General Characteristics of Food and Food Species

The black gibbons were seen to feed on fruits, leaves (both mature leaves and young leaves), flowers, buds and shoots (of both leaves and flowers). They were also observed to eat insects and other animal foods (Chen, 1995). However, animal feeding is difficult to record, as the method used is not as good as when recording plant parts (Palombit, 1997). Since no sample record is available for feeding on animal foods in this study, only feeding on plant parts is presented and discussed. But brief comments on animal food are presented in **6.8**.

Most plant species eaten by gibbons are seed plants, especially angiosperms. Some ferns were also eaten (only young leaves recorded). Two fern species were recorded and identified, *Vittaria flexuosa* (Vittariaceae) and *Lepisorus thunbergianus* (Polypodiaceae). The food types are listed in **Table 6-1.**

Table 6-1. The food parts eaten by black gibbons.

Species name	Drupes	Berries	Other fruits	Seeds	Buds and shoots	Young leaves	Mature leaves	Flower buds	Flowers
Betula luminifera					y	y	y		
Spp. of Loranthaceae	y	y			y	y	y	y	y
Cerasus cerasiodes	y			y		y	?	y	?
Myrica esculenta	y								
Actinida spp.		y							
Ficus virens		y							
Elaeocarpus braceanus	y								
Kedsura coccinea		y							
Holboellia forgesii			y						
Rhus chinensis						y	y		
Michelia floribunda								y	y
Rhododendron delavayi								y	y
Manglietia insignis								y	y
Mallotus philippinensis						y			y
Meliosma kirkii						y	y		
Rhododendron decorum								y	y
Celastrus glaucophyllus			y						
Cinnamomum tamala	y					y		y	y
Litsea cubeba	y					y	y	y	y
Elaeagnus spp.		y				y	y		
Vaccinium mandarinorum		y							
Castanopsis orthacantha						y			
Prunus majestica	y					y			
Lyonia ovalifolia		y					y		

Almost no gymnosperm plants were recorded as food for black gibbons except the "pine" recorded by Zhang *et al.*(1995). However, in these good quality habitats, there are few gymnosperm plants. Only in disturbed habitats and the mountain ridge area were pine trees and some other gymnosperm plants available. Black gibbons at Kainanhe (coded KNH) were once observed resting and travelling in pine trees, but this have not been seen at Xiaobahe.

6.3.2. Fruit Types

The black gibbons like to eat ripe pulpy fruits. These include berry, drupes and the seeds inside. But their favorite is the meat of berry-like fruits. Some research suggested that the other fruits or part of the fruits, such as nuts, capsules, and nutmegs, were eaten by gibbons (Zhang *et al*, 1995), but their data may not be based on direct observation, since observation is difficult. Food such as nuts of Fagaceae and pine seeds, although of high food value, are likely very difficult for the gibbons to handle since they are very hard.

Figs are not very abundant in the home range of group B. The fig is usually a ball fruit, about 1 to 1.4 cm in diameter, weighing 1 to 1.5g. When the trees are in fruit, it is very abundant. They usually bear in the winter and spring, and fruit ripen and fall in July first, and then in October second.

The ripe fruit from the tree *Cerasus cerasiodes* were abundant during May, and into June. Group B rely heavily on it in these two months. It is the most important food species for the month of May, both during 1997 and 1998. The fruit is about 1 cm long, 1.5-2.0g, and with a rugby ball shape. The hard seed is about 2/3 of the whole volume of the fruit. The ripe fruit is not very sour, but quite sweet.

The fruits of species of the canopy-parasitic family Loranthiceae are small (about 50-70 mm long and 60 mm width), about half the size of the fruit of *Cerasus cerasiodes*.

They are of many shapes, some similar to pears, some to the rugby ball, some to a football, some with 1 or 2 seeds, some with no seed. The ripe fruit are sweet and tasty.

The fruit of *Myrica escalata* (red bayberry) is shaped like a ball, with the juicy pulp covering the seed in a thin layer. It is about 0.5 to 0.7 cm in diameter, about 0.8 to 1.5g per fruit, with a seed about 3/4 of the whole fruit. Ripe fruit is tasty.

The other fruits such as *Kedsura coccinia* have been identified as *Schisandra* in Haimoff *et al.* (1987a), and was presented in detail in their paper. The fruit of *Elaeocarpus* spp. has been described by Sheeran (1993). There are about 4-5 species of the same genus, the fruit size of each species being different. The biggest is something like 3x2x1.5 cm, the smallest is about 2x1.5x1 cm. Ripe fruit is delicious. Local people collect them for eating and for sale.

The biggest fruits are those of *Kedsura coccinea* and of *Hollboelia* sp.. The *Hollboelia* fruit has a thick and hard outer layers, with edible pulp and seeds inside. It is usually 8-10 cm long, 2-4 cm width, with non-uniform shape, but usually in a long ellipsoid shape. It can weigh more than 200g per fruit, with many seeds.

6.3.3. Leaves and Flowers

The gibbons also feed on leaves (both mature and young leaves), flowers, and the buds and shoots (young stems). Some transformed leaves (thick and white) of *Lyonia* in April and May, are also foods for gibbons in group B.

6.4. Diet — Plant Species

6.4.1. List of Feeding Species

The black gibbons can adapt to a lot of different sites. Although the habitats are of similar appearance and plant family composition, the plant species composition and abundance can be different. The black gibbons seem to show that their habitat-specific adaptation strategies by the fact that plant species availability determines food eaten. Of course, this should be confirmed by more study at more sites, but some data are already available. For all food species feeding by black gibbons in Yunnan are listed in **Appendix 1**, based on data from all field studies.

Here I first present a species list which the gibbons at Xiaobahe (mainly group B) feed on, and then carry out a comparison of the food species lists based on other study sites (Chen, 1995; Yang and Xu, 1990).

6.4.2. List of Food Plant Species for Group B

The **Table 6-2** is based on the present study during 1997-1998. The number of food species increased as the field time increased. The dominant important food species are the *Betula luminifera*, then the groups of parasitic species of family Loranthiceae. Other important species are *Cerasus cerasiodes, Myrica esculenta, Actinidia* spp., *Ficus* spp.. The importance of these species varied between years as **Table 6-2** shows (See more discussion in **6.6.3.**).

6.4.3. Plant Species Difference Between Sites

Chen (1995) has listed 33 species as food in his Table 9 (p91-2) for gibbons at Xujiaba, Mt. Ailao (subspecies: *H. concolor concolor*). Some species (*i.e. Hartia sinensis, Lithocarpus* spp.) also occur within the home range of group B, but, based on our observation, we cannot be sure whether the group fed on those species or not.

Yang and Xu (1990) have listed a much longer food plant table for black gibbons (*H. c. furvogaster*) in Mt. Bangma. Most of the plant species in their list cannot occur in the high elevational band at Xiaobahe.

Table 6-2. The most important food species and its order based on all samples lumped together for the year 1997-1998.

	Samples					
Species name	1997	%	1998	%	Total	%
Betula luminifera	238	36.3	307	38.5	545	37.5
Spp. of Loranthaceae	201	30.7	201	25.2	402	27.7
Cerasus cerasiodes	40	6.1	133	16.7	173	11.9
Myrica esculenta	71	10.8	0	0.0	71	4.9
Actinida spp.	32	4.9	11	1.4	43	3.0
Ficus virens	6	0.9	28	3.5	34	2.3
Elaeocarpus braceanus	0	0.0	23	2.9	23	1.6
Kedsura coccinea	18	2.7	3	0.4	21	1.4
Holboellia forgesii	1	0.2	18	2.3	19	1.3
Rhus chinensis	10	1.5	6	0.8	16	1.1
Michelia floribunda	0	0.0	16	2.0	16	1.1
Rhododendron delavayi	0	0.0	14	1.8	14	1.0
Manglietia insignis	5	0.8	6	0.8	11	0.8
Mallotus philippinensis	5	0.8	4	0.5	9	0.6
Meliosma kirkii	8	1.2	0	0.0	8	0.6
Rhododendron decorum	0	0.0	5	0.6	5	0.3
Celastrus glaucophyllus	0	0.0	4	0.5	4	0.3
Cinnamomum tamala	2	0.3	0	0.0	2	0.1
Litsea cubeba	2	0.3	0	0.0	2	0.1
Elaeagnus spp.	2	0.3	0	0.0	2	0.1
Vaccinium mandarinorum	0	0.0	2	0.3	2	0.1
Castanopsis orthacantha	1	0.2	0	0.0	1	0.1
Prunus majestica	0	0.0	1	0.1	1	0.1
Lyonia ovalifolia	0	0.0	1	0.1	1	0.1
Unknown	13	2.0	15	1.9	28	1.9
Total	655	100	798	100	1453	100

6.5. Diet- Time Ecology

6.5.1. Feeding Proportion of Different Food Categories

The feeding time proportion on each dietary item is presented in **Table 6-3** for this study and the other three studies. During 1997-1998, for group B, similar amount of time were spent feeding on fruits and leaves (and young shoots), 46% and 47% respectively; and 5.6% on flowers and flower buds, 1.3% unknown. Only 2 records possible animal food were obtained (0.14% of the feeding time), suggesting that at least the gibbon showed some possible insect-feeding behaviour (insect-checking and catching activities) (See **6.7**). If the data are separated for different years (**Table 6-4**), it seems that group B fed more leaves in 1997 (total 12 months), but more fruits in 1998 (9 months together). From the table, we can see that all studies suggest that the black gibbons in Yunnan are compensatory leaf-eaters, with leaves taking a high value (from 43% to 72%). The proportion of the leaves in the diet for black gibbons is the highest among all gibbon groups (siamang mean is 50%, Sear, 1994; the black gibbons here is 54%, all other gibbons are between 6% to 50%, mean 28%, see **Chapter 9** for more discussion).

Table 6-3. Comparison of dietary composition for the studies on black gibbons*

Dietary composition	Present study (1997-98)	Lan (1989)	Sheeran (1993)	Chen (1995)
% fruit	46.02	21	44	24
% leaves	46.91	72	43	54
% flowers	5.62	7.4		6
% arthropods	0.14	Not measured	Not measured.	14
% unknown	1.30	N.A.	13.	2

*For Sheeran (1993), the proportion are provide based on reorganized data. Her original data contains 36% for feeding (foraging) both fruits and leaves, so the total fruits including the pure fruit proportion (26%) plus half of the previous data (18%). The same apply to leaves. For Chen's (1995) data, the flowers are flower buds.

Table 6-4. Comparison of dietary composition for the studies on group B in different year.

Dietary composition	1989	1997	1998	1997-98
% fruit	21	40.8	50.4	46.02
% leaves	72	52.4	42.6	46.91
% flowers	7.4	5.5	5.7	5.62
% arthropods	0	0	0.25	0.14
% unknown	0	1.7	1	1.30

6.5.2. Time Variation Among Months

The feeding time proportion among different categories varied from month to month (**Figures 6-2** to **6-4**). From these figures, we can see that the group B fed mainly on leaves, with less fruit in the diet, in March in both two years. There are four months in 1997 across the year and 3 months in 1998 across 9 months when the proportion of leaves in the diet is over 50%. These months can be defined as folivorous months. In the middle of the wet season (July to September), the group fed equally on fruit and leaves in 1997, and on almost all fruits in 1998 with small sampling. They might save energy for the period with a lot of rain by less active activities, such as rest.

For the months with most feeding data (March, April, May, June, 1997; February, March, May, June 1998), four months rely mainly on leaves (March and April, 1997, February and March 1998), and three month mainly on fruits (June 1997, May and June 1998), and one month has similar proportions in the diet (May) (**Figure 6-2**). For the other months, the gibbons feed mainly on fruits. This might be because, at this time, the gibbons were feeding heavily on the parasitic shrub fruits (spp. of Loranthaceae).

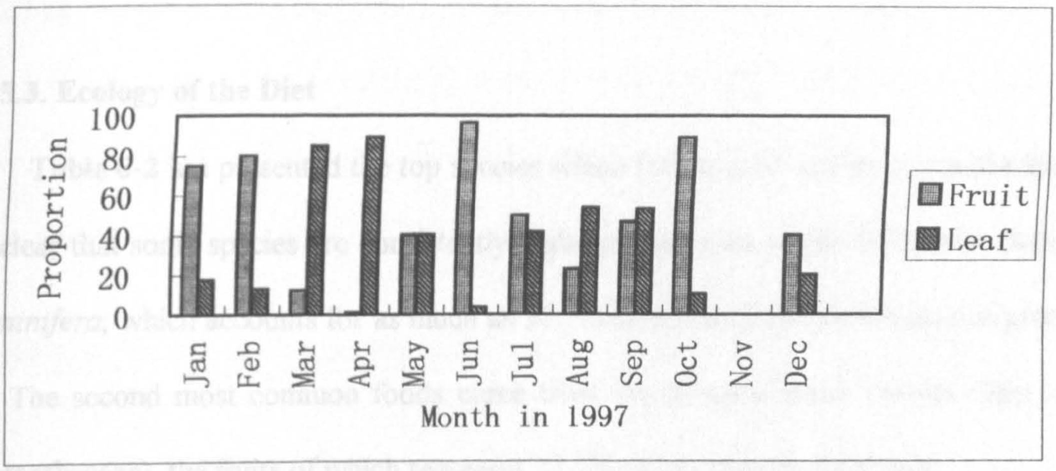


Figure 6-2. Food type variation during the year 1997.

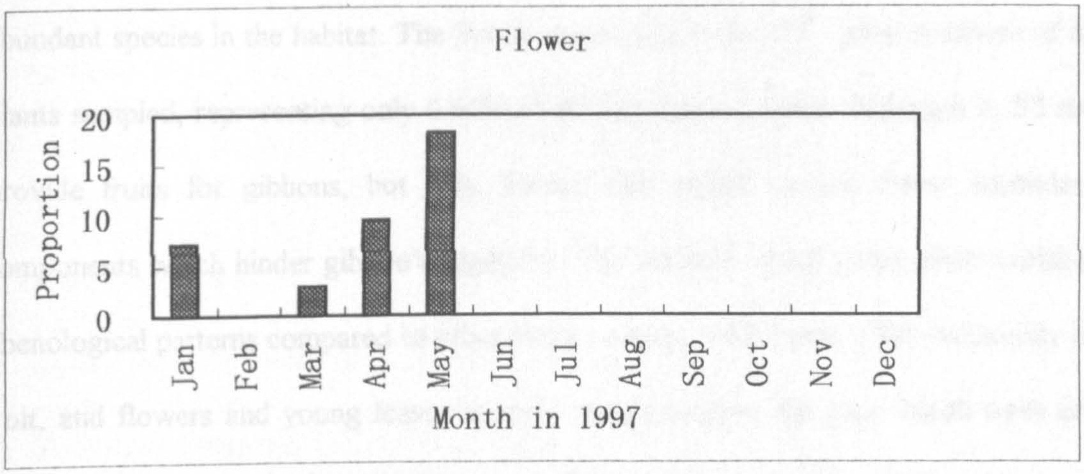


Figure 6-3. Flower variation in the diet in 1997.

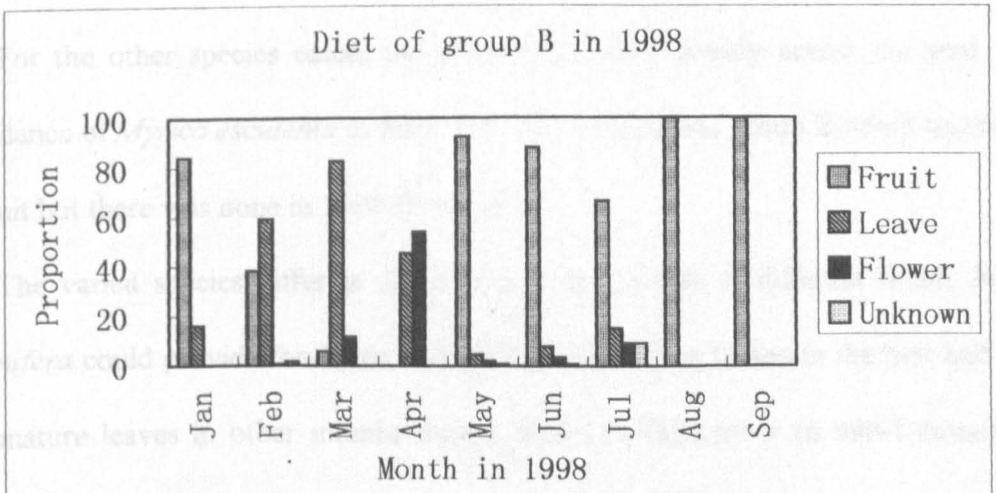


Figure 6-4. Food type variation during the year 1998.

6.5.3. Ecology of the Diet

Table 6-2 has presented the top species which the group B fed on. From the list it is clear that some species are consistently high-ranking, such as the birch tree, *Betula luminifera,* which accounts for as much as 37.5% of the total diet in the case of group B. The second most common foods come from the parasitic scrub species (Spp. of Loranthaceae), the fruits of which represent 27.7% of the total feeding time.

Why are these group B's staple foods? These species are not among the most abundant species in the habitat. The *Betula luminifera* is the 12th most common of all plants sampled, representing only 0.64% of all tree stems present. Although it did not provide fruits for gibbons, but only leaves, they might contain fewer secondary components which hinder gibbon's digestion. The parasitic scrub group show variable phenological patterns compared to other forest species, which ensure the availability of fruit, and flowers and young leaves at most months across the year. Birch trees are patchily distributed throughout the study sites, but the parasitic plants group are uniform in pattern (**Table 6-5**).

For the other species eaten, the proportion varies greatly across the year. The abundance of *Myrica esculenta* in June 1997 encouraged that group B relied heavily on its fruit but there was none in 1998 (**Table 6-2**).

The varied species differ in what foods they provide at different times. *Betula luminifera* could provide foods for most of the year: young leaves in the first half year and mature leaves in other months except from late-November to mid-February. In contrast, the important fruit provider, *Cerasus cerasiodes*, usually provides fruits during May to July only.

The food preference on different species are different from species to species: not all fruit providers are of high electivity, and not all leaf-providers are of low electivity. If this is not the problems of the fruit itself, then it might depend on the gibbons' preferences (**Table 6-5**). Most preferred food species are patchily distributed (10 in 14 with positive electivity index, see **Table 6-5**).

Table 6-5. The distribution pattern and electivity of plant species with food value.

Species or species group	Number in 2 ha	Morisita index	Pattern	Ei
Betula luminifera	5	2	p	0.98
Cerasus cerasiodes	6	0	p	0.96
Spp. of Loranthaceae	48		u	0.86
Ficus virens	3	6.7	p	0.83
Elaeagnus spp.	1		p	0.79
Mallotus philippinensis	4	10	p	0.79
Rhododendron delavayi	3		p	0.76
Myrica esculenta	16		p	0.75
Rhus chinensis	4		p	0.72
Michelia floribunda	1		p	0.67
Actinidia spp.	122		u	0.21
Elaeocarpus braceanus	15	6.86	p	0.18
Kedsura coccinea	70		u	0.13
Holboellia forgesii	69		u	0.08
Rhododendron decorum	3	4.10	p	-0.20
Cinnamomum tamala	7	0.95	p	-0.52
Celastrus glaucophyllus	60		u	-0.55
Litsea cubeba	12		p	-0.59
Manglietia insignis	48	1.95	u	-0.65
Meliosma kirkii	40	3.31	u	-0.68
Prunus majestica	17	1.62	u	-0.90
Lyonia ovalifolia	20	20	u	-0.91
Vaccinium mandarinorum	48	11.93	u	-0.92
Castanopsis orthacantha	29	6.99	p	-0.94

6.6. Diet Variation and Food Availability

The important plant species for group B varied from month to month, and to some extend from year to year. The cause is that the food availability varied from season to season, so the dietary proportion of fruits and other parts followed a similar pattern.

6.6.1. Monthly Variation

Based on **Figure 4-9** to **4-12**, it seems that fruit availability is most poor during March and April each year. Instead of feeding on fruits, group B ate a lot of leaves and leaf shoots during this lean period (**Figure 6-2** *vs*. **Figure 6-4**).

In general, if compared to the proportions fruits and flowers, leaves and shoots account for a very high proportion of the diet, especially during the dry season. During mid to late dry season, all ripe fruits have been lost or decayed, most species of trees and lianas are just beginning to regenerate with leave buds and flowers, with fruits still under development (**Figure 4-9** and **4-10**).

During May, at the end of the dry season and the beginning of the wet season, some fruit is ripe enough to be eaten, such as fruits of *Cearsus cerasiodes* and *Myrica* spp.. So at this stage, group B devoted a lot of time to eating those fruits. In May and June, it is not difficult to find the group, since they visited fruit trees of *Cerasus cerasiodes* and *Myrica* often. At this time Group B consumed most fruits and had little or no leaves in their diet.

In other months of wet season, group B was not observed eating fruits and leaves so intensively and they are become more and more difficult to be found. Possibly because the food patches are smaller or they are not preferred food items either for unripe or for quality and quantity, or for they have more choice available. From our phenological analysis, fruits are more evenly distributed around the home range in wet season.

At the end of the wet season and the early dry season, the fruits are still available and quite abundant. The fruits are not so patchily distributed as during the wet season, but much more uniformly, so the gibbons showed similar feeding pattern, foraging quietly under the canopy.

For the year round, especially in the middle of the dry season, during December, January and early February, group B seems to spend a lot of time feeding on small fruits from a few parasitic species (of the Family Loranthaceae), which are usually available year round (**Figure 6-5**). Their diet in this dry season period, complemented by the leaves from some liana species.

From time to time, but mainly in the first half year, the gibbon group was also found to eat some flowers. They are probably compensatory food when the favourite food is not abundant. The flower abundance is illustrated in **Figure 4-12** in **Chapter 4.**

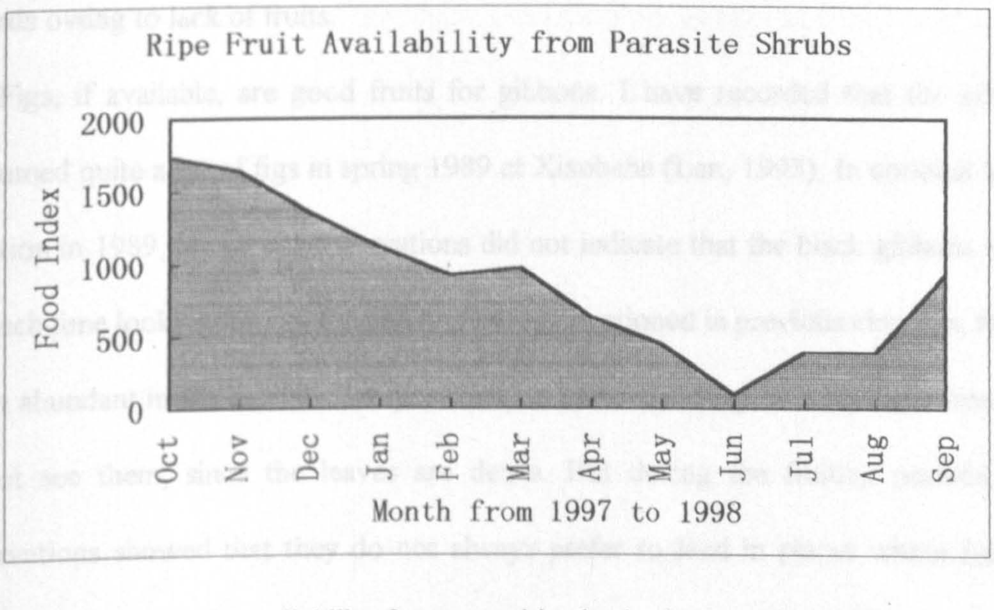


Figure 6-5. Ripe fruits availability from parasitic shrubs from 1997 to 1998.

6.6.2. Seasonal Diet Variation

From **Tables 6-2** and **Figure 6-2** to **6-4**, we can see that the group B had different feeding strategies according to the food availability in different seasons. The fruit availability is much richer after the end of dry season, and lasts until the beginning of the following dry season. At this time, group B usually fed on fruits, and only partly on leaves. From the proportion ratio for each category, we can conclude that the dry season or at least the late dry season is mainly poor for the gibbons, since not enough high quality food is available for the group.

6.6.3. Yearly Variation

The diet are also varied from year to year based on the food availability. The genus *Elaeagnus*. is an example. The species *E. conferta* was an important fruit provider during February and March in 1989, but not the same groups during 1997 and 1998 since no fruits are available. The shrub (sometimes big tree) *Myrica elascata* fruits were very important food sources for the group in June 1997, but not in 1998, without records owing to lack of fruits.

Figs, if available, are good fruits for gibbons. I have recorded that the gibbons consumed quite a lot of figs in spring 1989 at Xiaobahe (Lan, 1993). In contrast to the situation in 1989, my recent observations did not indicate that the black gibbons spend as much time looking for and feeding on figs. As mentioned in previous chapters, the fig is not abundant in the habitat. One possibility is that when they feed on these trees, we cannot see them, since the leaves are dense. But during the fruiting periods, our observations showed that they do not always prefer to feed in places where figs are available.

The diet variation between seasons and years in the top ranked food species suggests that the black gibbons are highly opportunistic foragers, and feed on items as and when they become available. Most food species are characterized by inconsistent fruiting patterns, such as figs (*Ficus* spp.) and parasitic shrubs (Family Loranthaceae). Most of these species are patchily distributed in space (**Table 6-5**). An opportunistic strategy of foraging is required under such conditions if the habitat is to be efficiently exploited as in other primate species showed (Barrett, 1995).

6.7. Food Preferences and Dominance

6.7.1. Food Species and Preferences

Among the plant species on which group B fed, a small number of species were of high value to black gibbons (**Table 6-2**). One is a deciduous tree, *Betula luminifera*, which provides a lot of young leaves in the spring and mature leaves as food afterwards. In winter, after December, the leaves of this tree species fall, and no more leaves are left. So during this period, it is less important to the gibbons.

The parasitic species of the family Loranthaceae include at least 3 species at Xiaobahe. As reported by Peng (1997), there are about 12 species in the area of Mts. Wuliang (**Table 6-6**). According to the description of the fruits they bear (berries or drupes), fruits from all the species of the family can be used as food by gibbons. ***Viscum articulatum***, one of the important fruit producers for group B, is very widely distributed in the forest at Xiaobahe and the adjacent areas we visited. But it is not very popular at Xujiaba.

As reported by Peng (1997), there are 28 species of the fig species (genus *Ficus*) in Mts. Wuliang. However, most are distributed at low altitudinal bands. But at least 2 species are available at Xiaobahe, *F. neriifolia*, *F. yunnanensis*. In the habitat of one group, KNH1, we found that in the altitudinal band of 1700-2000, there are many more fig species. Local people suggested that the gibbons ate a lot of the fruits of figs. The group has been observed to eat a lot of fruits of other species (*e.g. Sorbus rhamnoides*) by my assistant in the past. In addition, there are a lot of other species which are possible foods for the group, such as *Eriobotrya bengalensis angustifolia*.

Table 6-6. The list of parasitic species which possibly provide food for gibbons in Mts. Wuliang*.

Species	Possible altitudinal band	Abundance degree	Feeding confirmed
Dendrophthoe pentandra	Unclear	Unclear	
Elytrathe albida	2000-2400	Common	p
Helixanthera parasitica	1100-2200	Very common	p
Helixanthera scoriarum	Unclear	Unclear	
Loranthus delavayi	2400-2850	Common	p
Scurrula ferruginea	1450-?	Unclear	
Scurrula parasitica	1100-2400	Common	p
Scurrula philippensis	?-2600	Common	y
Taxillus delavayi	1900-2650	Common	y
Taxillus sericeus	1500-?	Common	
Viscum articulatum	?-2800	Common	y
Viscum liquidambaricolum	1650-2100	Common	p

*All data from Peng (1997), the criteria are based on his descriptions. Feeding confirmed by direct observations (y-yes) or by checking the fruit types (p-possible).

Among all these species, we can calculate that the most important are the first few species in the list. They provide food all year around. Some of them are very important for some seasons when they are available. We got only one record of them eating young leaves, but not fruits of this species during our recent study period.

In 1998, *Eriobotrya bengalensis* bore more fruits than in 1997. Similar results were obtained for *Elaeocarparcus* spp.. In contrast, few fruits of *Myrica* were available in 1998, but production was very rich in May and June in 1997. It accounts for almost all feeding time in the few observation days during this period (especially June 1997). Figs were also more abundant in1997, but few in 1998. So long-term monitoring of the plant food production will be very interesting and will shed more light on the survival strategies of black gibbons.

Table 6-7. The most important food species for each month for black gibbons in 1997

Month	First species	Second and third species
January	Spp. of Loranthaceae	*Ormosia olivivacea*
February	*Ficus virens*	*Ormosia olivivacea*
March	*Betula luminifera*	Spp. of Loranthaceae
April	*Betula luminifera*	*Actinida* spp.
May	*Cerasus cerasiodes*	*Betula luminifera*
June	*Myrica esculenta*	Spp. of Loranthaceae *Ficus virens*
July	Spp. of Loranthaceae	*Betula luminifera*
August	*Meliosma kirkii*	Spp. of Loranthaceae *Actinida* spp.
September	*Betula luminifera*	*Actinida* spp. (glauso-callosa)
October	*Kedsura coccinea*	Spp. of Loranthaceae
December	Spp. of Loranthaceae	

Table 6-8. The most important food species for each month for black gibbons in 1998

Month	First species	Second species	Third species
January	Spp. of Loranthaceae	*Kedsura coccinea*	
February	*Betula luminifera*	Spp. of Loranthaceae	
March	*Betula luminifera*	*Michelia floribunda*	
April	*Betula luminifera*		
May	*Cerasus cerasiodes*	*Ficus virens*	
June	Spp. of Loranthaceae	*Elaeocarpus braceanus*	*Rhus chinensis*
July	Spp. of Loranthaceae	*Betula luminifera*	
August	*Elaeocarpus braceanus*		
September	*Ficus virens*	*Actinida* spp.	

6.7.2. Dominant Food Species of Each Month

The dominant tree species changed from month to month. **Table 6-7 and 6-8** show the first few most important species as food provider to group B. In the first half year, before the wet season, the *Betula luminifera* and the parasitic species are very important food providers.

6.8. Animal Food

Animal food, although not high, always occupied an important part in the life of the gibbons' food (Chivers, 1984), especially in some species like kloss gibbons (Whitten, 1982). The black gibbon was observed to eat some animal food too (Chen, 1995).

Animal food can provide important nutritional components such as protein and minerals for the gibbons. Fruits cannot provide all the protein necessary for the gibbons. In some species, when the gibbon requirement for protein sources is not enough, they tend to consume more young leaves, *i.e.*, siamang (Chivers, 1974). If fruits are sufficient, the animals will eat more fruit, instead of leaves, as a recent long-term study on both lar and siamang in Sumatra (Palombit, 1997) has shown. Both siamang and lar showed flexibility in their diets. It seems that diet compositions are habitat specific, based on the sites and seasons; as Palombit (1997) pointed out figs are much more abundant at study site in Sumatra sites than the one in Malay Peninsula.

Some observations suggested that black gibbons might look for insects for food, too. On a few occasions, we have recorded that they checked the bark (usually rotten, and possibly with ants inside) of a dead tree. But we cannot verify that they found anything in it which they ate.

The direct evidence for animal components in their diet comes from feces analysis. In dry season, I collected 5 piles of faeces from the same group. I could not see any remains of insects. When put under the microscope, however, we found one skeletal fragment from an insect, but the species cannot be identified. Feces analysis cannot give an estimation of the proportion of insects consumed.

It is difficult to collect gibbons' feces in the forest, since we cannot follow them under the tree. Although it is possible sometimes to find feces where there is a lot of stones on the ground in the dry season, it is not possible in the wet season. But more insects are active during the wet season, usually the hottest time in the year. Another possibility is that when they feed on leaves, the gibbons chew and swallow the leaves with some insects on them.

From faeces analysis, the black gibbons feed on figs in the dry season (not similar to the results of Sheeran, 1993). According to our observation in the field, 70% to 80% of figs are parasitied by insects called *Ceratosolen* sp. of the family Agaomidae, so it seems that the black gibbons must consume some animals (Prof. Darong Yang, personal communication).

Apart from the animal parts mentioned above, the feces also contain some other remains. The bulk of the feces consists of leaves of trees and lianas, or plants belonging to Orchidaceae, such as *Dendrobium* sp (possibly *Dendrobium kancockii*). Since the feces quantity is too small, no quantitative analysis has been carried out. The leaves documented from the feces are supported by the direct observations of their feeding on the leaves.

6.9. Summary

In this chapter I have discussed the diet, food species, feeding behaviour variation and preferences of black gibbons. The focal group was both frugivorous and folivorous in general; they consumed significant amounts of leaves during times of relative fruit scarcity.

Black gibbons fed on many plant species, but the majority of the diet was make up of a few non-dominant and relatively rare species which were available at temporally distinct periods across the year. Most of the important black gibbons fruit species are ephemeral in nature, found in relatively low density, and distributed patchily across the home range. Variations of diet exist from month to month. Yearly differences is also existed.

Some stable and preferred food species (or taxa groups), either providing fruits or leaves, are available for the groups. *Betula luminifera* leaves were the most important components of the diet during all my study years. This species shows little inter-annual variation in phenological patterns. For fruit source (and leaves and flowers source), a species group parasitic species of Loranthaceae, is stable food provider for the gibbon group too. As mentioned in the previous chapter, fruiting individuals of these species were uneven and non-synchronized. They do not show apparent inter-annual variations in their phenological patterns. Other fruit sources, such as *Cerasus cerasiodes* species and *Myrica esculenta*, do show apparent inter-annual variations in abundance, and with highly synchronized phenological patterns.

Dietary shift is common in black gibbons as the proportion of time spent among fruits and leaves varied from month to months. The highly folivorous diet might reflect an adaptation to the poor quality habitat in most northerly ranges, and may also related to the high proportion of polygynous composition in this species (**Chapter 3**).

In the next chapter I will further explore the ranging behaviour of the black gibbons. How do spatial distribution and temporal differences of the main food resources affect black gibbons' habitat use. In doing so I will detail the home range of the group and examine a number of other ranging parameters in relation to variation in temporal and spatial resource availability.

CHAPTER 7. RANGING BEHAVIOUR

7.1. Introduction

Lesser apes are generally associated with relatively tall, climax tropical forest types throughout Southeast Asia. Nevertheless, previous studies and short term surveys have revealed that *Hylobates concolor* is found at least temporarily in other forest types, for example, in dry deciduous forest. Primate surveys within Yunnan had revealed the presence of *Hylobates* in the following types of forest: monsoon broadleaf forest, mountain humid broadleaf forest, and some mixed forest (**Chapter 3 and Chapter 4**). Unfortunately, only very few data are available about the ranging behaviour in this species. Only two home range data are available, one for Xiaobahe group based on a short study 10 years ago (Lan, 1989), and a more recent one for Xujiaba group (Chen, 1995). Liu *et al* (1989) give an estimate of 362 ha for home range size, but it seems rather large and might be an overestimation. However, although, no specific data are given, other studies suggest that black gibbon's home ranges may be in the order of 100 to several hundred hectares (Liu *et al.*, 1989). Similarly, only two estimates are available for day journey length (Chen, 1995; Lan, 1989).

In general, the major influence on primate ranging behaviour is thought to be food abundance and distribution (Bennett, 1986; Clutton-Brock, 1977). Temporal variations in the availability and distribution of preferred resources may also shape primates' ranging patterns (Agetsuma and Noma, 1995; Defler, 1996; Olupot *et al.*, 1997; S.Y. Zhang, 1995), and ultimately affect the size and shape of home range (Harvey and Clutton-Brook, 1981). Nevertheless, other factors are also known to affect primate ranging behaviour, for example, the location of water resources (Altmann and Altmann, 1970), position of sleeping sites (Rasmussen, 1979), climatic extremes (Chivers, 1974), and the need to patrol boundary areas of the home range (Goodall, 1986).

In this chapter, I will examine the habitat use of the focal black gibbon groups. The overall picture and seasonal differences will be interpreted in light of monthly variations in the relative abundance and distribution of fruit resources. The size, shape and habitat distribution of the group's home range will be detailed. I will also examine several other aspects of the black gibbons' ranging behaviour with respect to resource availability and distribution. Finally, these finding will be compared with those from other long-term *Hylobates* studies. I will attempt to characterise the ranging behaviour of black gibbon in relation to the spatio-temporal distribution of their food resources and feeding behaviour. Following a review of the methods used to measure day journey length, home range and ecological variables, I go on to describe, and compare these with data collected during previous studies.

7.2. Method

I used the People's Liberty Army (of China) 1:50000 map with topographic data for survey and intensive study use. During intensive study period, the original map was amplified large enough to record the changes of position of gibbon individuals to an accuracy of 10-20 m. Later, a transparent one hectare grid map was superimposed on to these maps and provided the basis for plotting and quantifying the majority of the various ranging parameters presented below. This was a necessary analytical step because the trail system was too simple; most of the time I could not check the trail to get the fixed point of the gibbon's location since I usually observed the groups above the canopy and outside the forest. I can only estimate the point by eye, recognise the characteristics nearby and estimate the position on the map (*i.e.* a valley, position of waterfall or prominent tree which is easily recognised). The trail system has not been designed to create uniform blocks owing to the rugged terrain and the realities of building a trail system in dense broadleaf forest with dense shrub.

Table 7-1. The habitat types for the black gibbon group B at Xiaobahe.

1). Good Valley forest: Usually evergreen,(moist), without or with rare deciduous tree, tall, high, with continuous canopy and looks evenly, high canopy cover. Usually in the valley on stream bed, near the stream.

2). Poor valley forest: evergreen and deciduous tree are mixed, tall, unevenly continuous canopy with two or more layers, with high canopy cover in wet season, but not in dry, especially early dry season. Usually with a lot of *B. Luminifera* tree.

3). Shrubs in valley: It is in valley, usually tree is rare, with a lot of shrubs, short in height, with or without many vines.

4). Shrubs on peak and slope. Tree (shrub) might be small, short, but usually dense, continuous canopy, with some *B.luminifera* tree (small).

5). Good slope forest. Evergreen forest on slope, with good canopy cover, high and good looking.

7.2.1. Habitat Types

The mid-mountain humid evergreen broadleaf forest is quite homogeneous. Although it can be classified to several types by botanists, it is difficult to used those categories in small area (**Chapter 4**). In this study I divide the habitat into 5 categories by rough physiogonomy analysis (including landscape location and human disturbance), as well as by altitude in order to determine how do the gibbon select habitat (**Table 7-1**). If one type occurred in a 1-ha plot in majority, then this plot was labelled by the type. Plots were also divided by altitude, according to the location of majority of the plot: <2300m, 2300-2400 m, 2400-2500 m, >2500 m.

7.2.2. Day Journey Length

The main method to measure day journey length is based on direct measures of distance travelled by following the groups moving from one location to another location on map. Usually the female's route was checked as the main route, because the adult females can be easily recognised. This method inevitably gives a quite accurate result. But this method limited the data used to those days when all day follows were possible. To increase sample size, days were included even if there was a break providing the break was not greater than 3 hours. In these cases, we have extrapolated by connecting the two points across the time gap.

I also measure the direct distance from one sleeping (or calling) point to the next sleeping (calling) point recorded the next morning. Here I assumed that the sleeping points are not far away from the points where they called that day, and this was verified by some whole day follows: The distance between the sleeping site and early morning (at dawn) calling site on the second day is about 0 to 30 m based on some successful early morning observations when the group engaged in morning song. In some months, these data are not possible to get, so I just recorded any two points 24 hours apart, such as the points at 1pm for the first day to the point at 1pm of the second day.

Since the day journey length is not complete for most days, and difficult for comparison, I also measure the daily averaged travelling speed. Mean daily speed of travel was simply day journey length divided by total travel time.

Since the slope varied, in order to calibrate the plane distance, we sampled 30 points in the home range of group B, and finally calculated 26.5° as the average slope gradient. So all distance and areas here are corrected by multiplying them by cos26.5°.

7.2.3. Home Range Size and Use

From the records on the map of the groups' ranging route everyday, the 1-ha plot map was used to count the hectares where the group ranged. The first measure was simply the number of one hectare cells the gibbons were observed to enter during the course of the study period. This measure is fairly standard in the primate literature (Wallace, 1998, S.Y.Zhang, 1995), but tends to overestimate home range sizes because large sections of cells (inside the home range areas, as well as especially border cells) are often not used by the focal group.

The second measure used all locations in border cells to create a rough perimeter line around the home range. This map was then used to estimate the proportion of each border cell which was included within the group home range. I calculated the proportion of each habitat encompassed within the home range by allocating a percentage cover score (to the nearest 5%) for each habitat within each cell. Habitat scores for border cells could only total the proportion of that cell contained within the perimeter based range map.

Day range was calculated as the number of quadrats in which black gibbons were observed during scans occurring on an full-day follow. Monthly range was calculated as the absolute number of cells entered by the group during all observations, although this measure should be interpreted with caution because the sample size was small in most months and not uniform across the months. I also calculated a mean monthly value for a number of ranging parameters (*e.g.* day journey length, day range). **Figure 7-1** shows the numbers of samples and plots numbers used by the group B in the two years monthly.

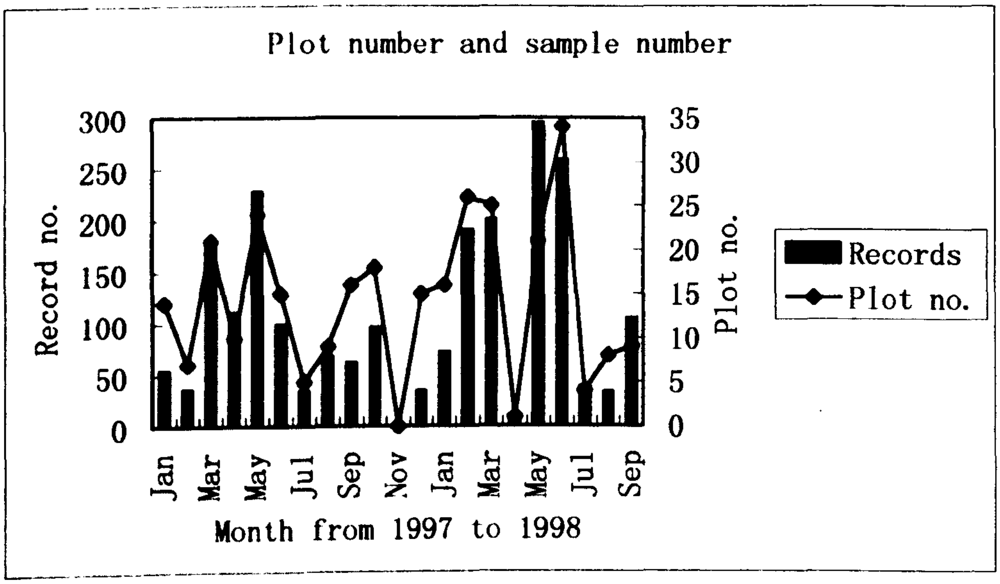


Figure 7-1. The samples distribution and the plots used by the group B.

I use core area to describe the focal gibbon groups' ranging use. Following Barrett (1995) I compared the distribution of sightings across the one hectare cells with those expected assuming a uniform sighting distribution. I use the numbers of scans recorded in each cell the gibbons ranged inside to calculate the percentage of use for each cell in each sample month and produced an overall value for each cell by averaging the monthly percentage. Those cells in which black gibbons' residence exceeded the expected uniform percentage value were considered part of the core area.

I used Morisita's index (Poole, 1974; Robinson, 1986) to measure the patchiness of quadrat occupancy:

$$I_\delta = N\Sigma n_i(n_i-1)/n(n-1)$$

Wherein N is the number of quadrats used, n_i is the occupancy record in the ith quadrat, and n is the total number of occupancy records. The more patchy the quadrat occupancy, the bigger the index.

7.3. Travelling Time Ecology

The gibbon group B in the present study spent an average of 22% of their time travelling (**Table 7-2**). This figure differs markedly from those given in previous studies of the same gibbon group, and from groups studied by other scholars (Chen, 1995; Sheeran, 1993) (**Table 7-2**). The differences between my two studies may be attributed to the effect of year differences (**Table 5-6**). My previous study (Lan 1989) was a short term study and data were limited to the dry season (February and March), but the present study included data across all seasons in two years. If compared with last study using only dry season data, the moving time proportion is similar (15 % for this study, see **Chapter 5, Figure 5-8**) but yearly difference still exists (**Table 7-3**). Differences in group size may also have been important: the higher travelling time in the present study is in accord with the larger group size. Again, as mentioned in the previous chapter, this discrepancy can be partly attributed to differences in methodology, since observational techniques and sampling schedules used is not the same in these studies. Sheeran's (1993) data are mainly from *ad libitum* samples: activities such as travelling maybe easier to detect. Chen's (1995) group was smaller than mine, but travelled more and longer in distance each day: this might be related to the relatively poor quality habitat at Xujiaba, compared to group B at Xiaobahe.

Table 7-2. Comparison of ranging behaviour for the four black gibbon studies*

Variable	Present Study	Lan (1989)	Sheeran (1993)	Chen (1995)
% travelling	22	14	32[a]	28
Day journey length	838.7	795	No data.	1306
Quadrats (1-ha) used per day	6.5	7.4	No data	No data
Home range size (ha)	50-60	44-49	No. Data	87
Group size	7 (8)	4	5.4 [b]	4

*a. travelling (14%)half foraging (36%); b. Averaged group size for her research groups.

Table 7-3. Comparison of ranging behaviour for the two studies on group B in the same season (February and March) in 3 different years.

Variable	1989	1997	1998	1997-98
Range size observed (ha)	14	18.5	24.4	22
Day journey length (ha)	795 (n=5)	735.5 (n=11)	898 (n=19)	838 (n=30)
Group size	4	7	7	7

7.4. Day Journey Length

The group B usually travelld slowly, with an averaged speed of 103 m per hour and day journey length 862m based on data for all observation days. If only calculated those days of more than 5 hours observation, the day journey length averaged 837±458 m, range 210 to 1820 m (n=39).

The speed varied both between days and across the day. Sometimes the gibbon travelled very slow and short, but sometimes very fast and long, depending on the food types (ripe fruit and young leaves) and availability. If food was abundant, they might stay nearby after a feeding bout, and later visit the source again and again (usually when young leaves are available); or they can travel to other sites for some distance and come back to feed on it (usually when ripe fruits available). They can stay in one place (*e.g.* in 20x20 m^2 area) all day, if the place has dense trees nearby and abundant food, usually in the dry season (February to March) and the site with abundant young leaves (usually *Betula luminifera* and some liana species). When they want to change for another abundant food patches area, they travelled far in a short time, something like 500 meters or longer in less than half an hour. On most days, they stayed near a food abundant area (which part of the home range depended on season and fruit type and abundance), and travelled up and down nearby for a few days, and showed an average-length day journey length.

The travelling speed varied from day to day, and from month to month. In dry season, the averaged speed is 86.7 m per hour (n=125.45 hour in 15 days), and in wet season, 115.3 m per hour (n=156.92 hour in 18 days). But the difference is not significant (t=-1.885, df=31, P=0.073). This means in both seasons, the gibbons' travelling speed varied greatly. When several continuously observed days data analysed together, I found that the group used the habitat patchily, and only when they changed home range parts, they travelled a long distance. Within the abundant food patches in the some parts of the home range, their travelling speed was slow and daily journey length was short.

The day journey length in wet season is similar to that in dry season (X^2=1.335, df=1, P=0.248). The average distance between two sleeping site is 335 meters (n=32) in 1997. Either based on monthly data, or day by day, the distance and rainfall are not significantly related (r_s=0.136, n=15, P=0.360, for months; r_s=0.113, n=39, P=0.535, for days).

In general, the day journey length in black gibbons is short if compared with other gibbons, but similar to that of siamang. The high folivorous diet might be highly related to their short day journey length, because they no need to travel far to get enough food to eat, for the leaves are abundant, in general.

7.5. Home Range Area

7.5.1. Period I (1987-1989)

In 1987 to 1989, I estimated that group B ranged in an area of about 49 ha if all plots available to them are included (Lan, 1989). For most parts of the range area, we did not have observations on entry because of the limited observation time. In a previous paper (Lan, 1989), I divided the habitat into 3 sectors, 'a', 'b', and 'c' (**Figure 7-2**). In a two-year off-and-on field study beginning in October 1987, I only recorded that the group ranged in part 'b', but not in 'a' and 'c'. They were heard calling from sector 'a', but were difficult to find there. No evidence that they use sector 'c' (about 5 ha of forest) was obtained, and since sector 'c' is long and thin for the group to range inside, I hesitated to include it into their home range.

7.5.2. Period II (1997-1998)

In the present study period (1997 to 1998), I confirmed that all three sectors (a, b, c) are parts of the group's home range. They even ranged outside these three sectors into other areas we first thought unlikely that they would use. In summer (May and June) 1998, the group went further into that habitat sector (d) across Xiaobahe river, which was assumed to be the home range of group D in 1988 or possibly group F in 1997-1998. This sector is separated from the other parts ('b') of group B's home range, even at this time. The separation is a gap of 6-8 meters wide, with no trees or shrubs available 10 years ago. But now some shrubs have grown there and the gap is now in the canopy layer about 1-2 m above the ground. A similar gap (5-8 m) is present in another end of the home range, separating sector (e) from 'a'. The sector was possibly once part of the home range of group B, for local people and one of my assistants reported that one group (possibly group B) ranged there sometimes. Unfortunately we cannot confidently confirm that fact. Both these two sectors are connected with the ranges of other gibbon groups. In the past, gibbon calling has been heard in these areas, but "who is who" has never been made clear.

7.5.3. Home Range Size Estimate

The home range size can be determined from **Figure 7-2**. Including all plots of 'b, c, a', and those actually entered by groups in sector 'd', we estimated that group B's home range is about 88 1-ha plots. This area contains forest, shrubs around the forest and inside the patches, and the woodless land within the forest. The group was observed entering 73 quadrats during the two year study period (57 quadrats in 1997 and 62 in 1998). So we can assume that the home range of group B is at least 73 ha. The fact that a cumulative plot of quadrat use seems to be approaching an asymptote (**Figure 7-3**) suggests that most quadrats used by the group had been identified.

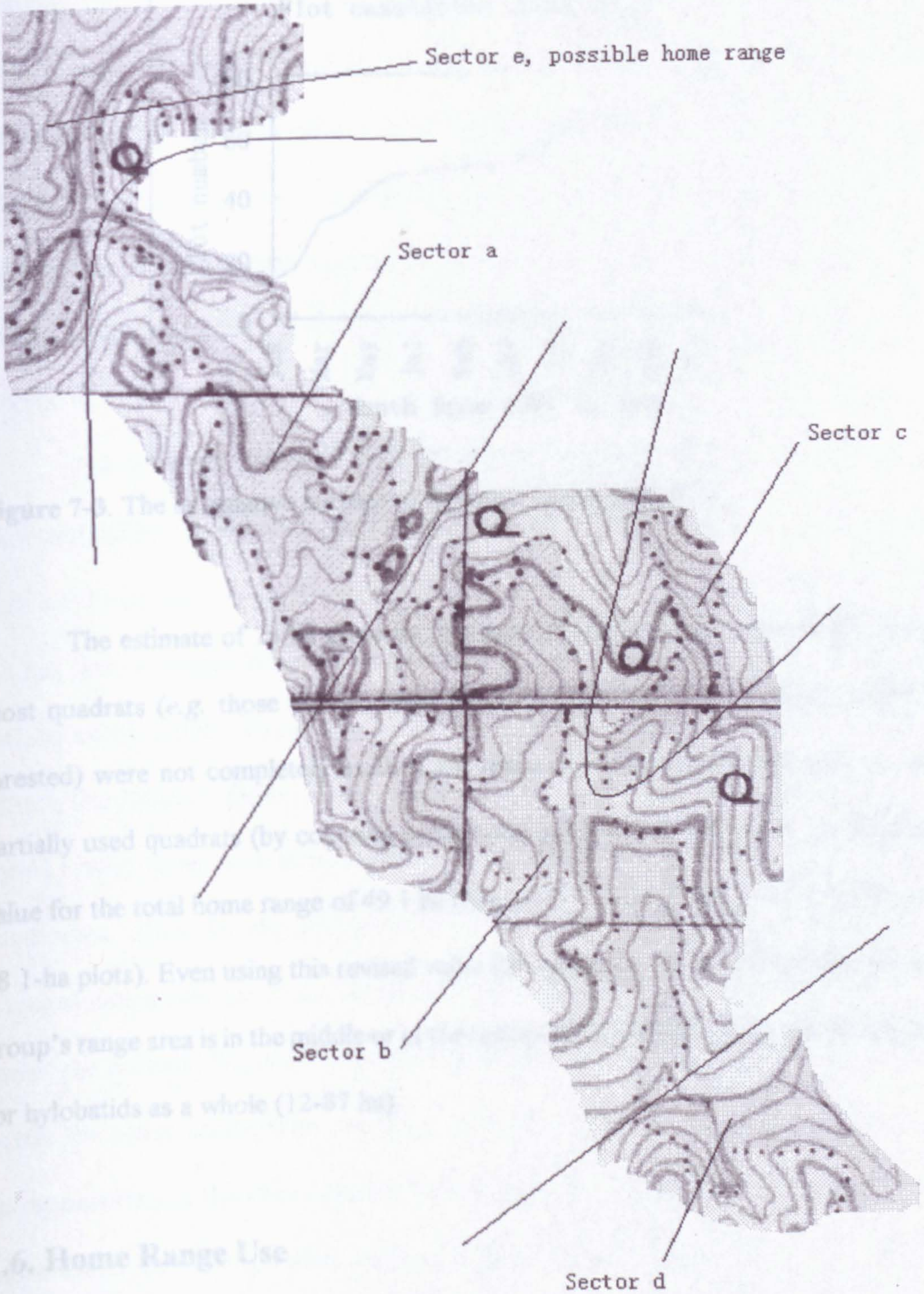


Figure 7-2. The home range of group B and its sector division.

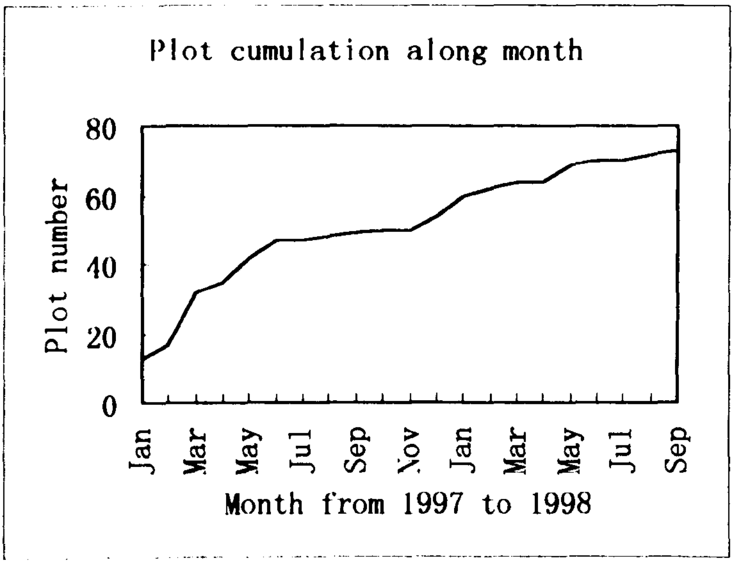


Figure 7-3. The cumulative number of the plots used by group B.

The estimate of 73 ha given by this method should be an overestimate because most quadrats (*e.g.* those on the range boundary or those that were not completely forested) were not completely used. If we adjust the estimate of range size for these partially used quadrats (by counting partly used quadrats as half units), we obtained a value for the total home range of 49.1 ha (based on 73 1-ha plots) or 54.9 ha (based on 88 1-ha plots). Even using this revised value for range size, it is still clear that the study group's range area is in the middle or at the upper end of the home range size distribution for hylobatids as a whole (12-87 ha).

7.6. Home Range Use

7.6.1. Habitat Selectivity and Core Area

Plots are not evenly used by the group. Some were used for more time. The frequency at which the black gibbons entered each cell of their home range differed significantly from an even distribution (X^2=4077.85, df=72, P<0.0001) through the two year. **Figure 7-4** assesses the overall intensity of quadrat use across the home range using five intensity categories: 1% and above of overall use, >0.4 to =<1% use, >0.1 to =<0.4% use, >0 to =<0.1% use and finally no use. Overall the pattern of range use could be described as clumped (Rasmussen, 1980), with several foci of intense activity distributed across the range. The difference between the observed and expected overall distribution of black gibbon sightings across the home range was significantly different from a uniform distribution (One-Sample Kolmogorov-Smirnov test, z= 5.916, n=88, P<0.001).

The number of one hectare cells where black gibbons range use exceeded the expected uniform distribution was 23 (26.1% of 88 ha home range estimated), and these cells can be considered 'core' area cells (see **Figure 7-5**). As we can see, the core plots do not form a concentrated area, but a long and thin shaped area which seems to be influenced by suitable forest for food and safety. Some parts are not connected with others, like isolated islands. These core plots were those with mixed forest types: dense forest (valley forest with some shrubs or other food trees, and possibly with abundant food trees, either *Betula luminifera* for leaves and those scrubs parasitic on it, or *Cerasus cerasiodes* for fruits, or with abundant liana species, or with all these). The lower the altitude, the more core plots there are. The gibbons also showed that they prefer the valley habitat over the slope or peak forest or shrubs, although some good forest occurred on the slopes (**Table 7-4**). Forest in the valley, including shrubs, provide more foods, as the vegetation study showed more food trees (*Betula luminifera* and *Cerasus cerasiodes* and others) occurred in these type of habitats, and they have larger dbh and higher production biomass (when measured as abundance).

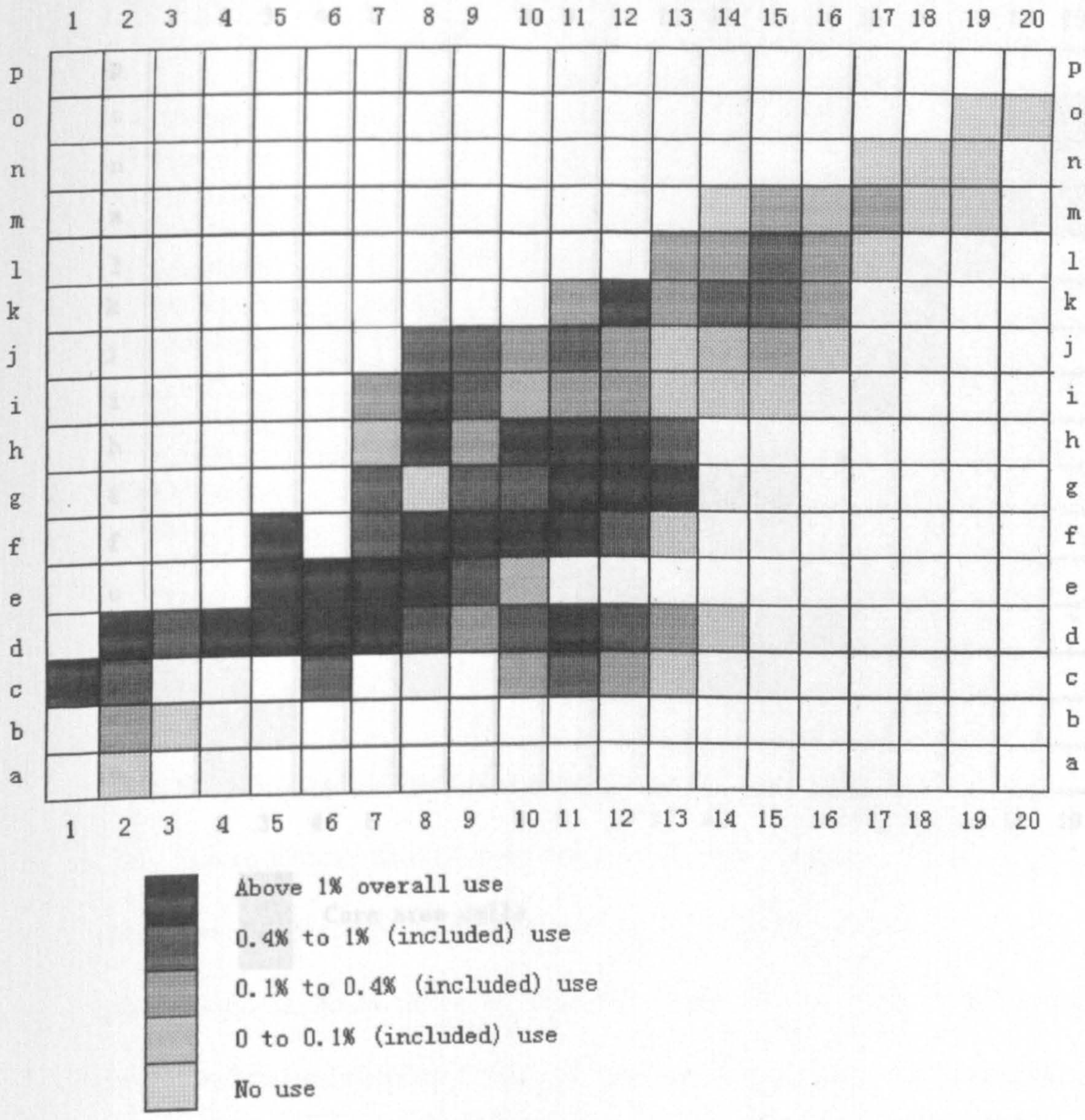


Figure 7-4. Overall intensity use of the quadrats in the home range of group B.

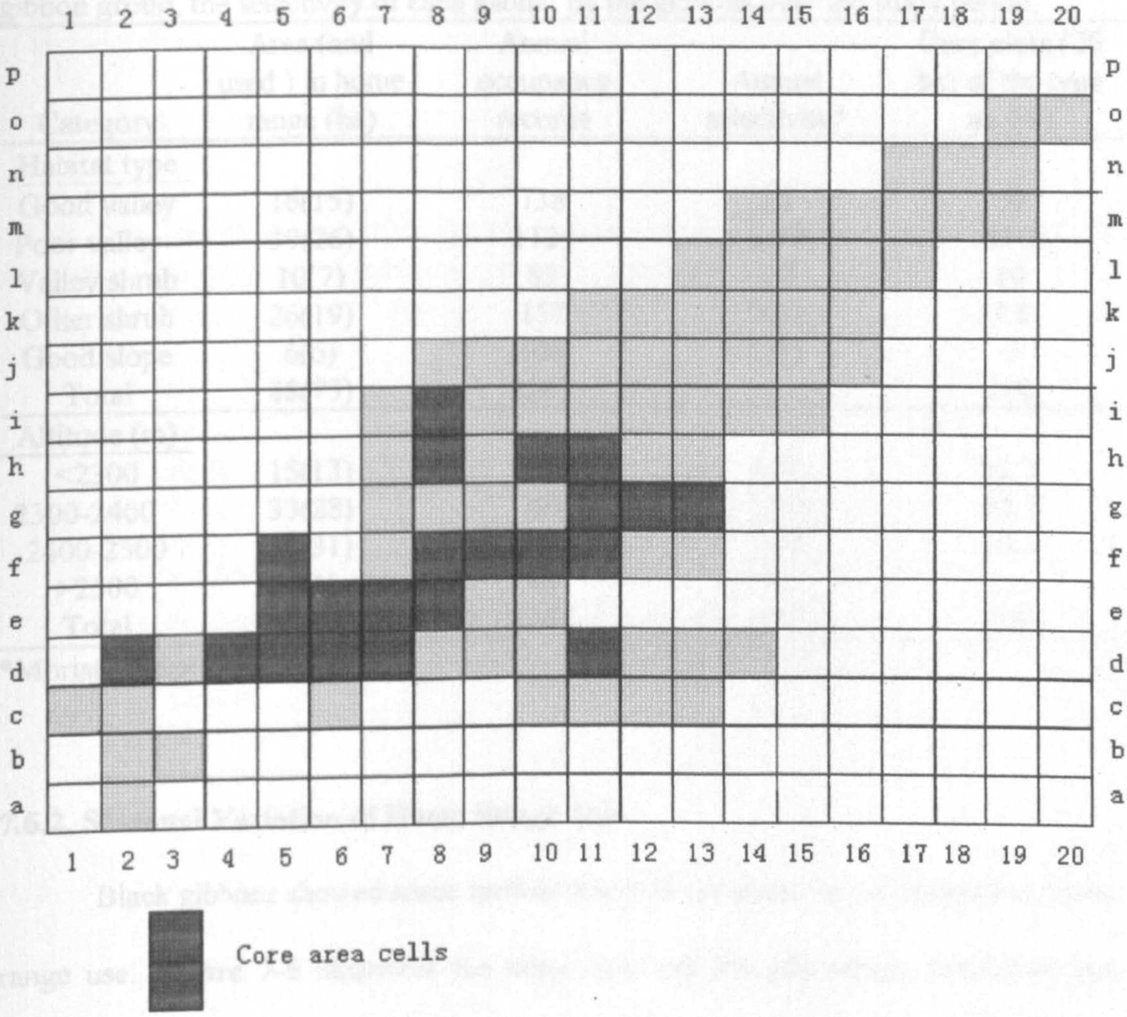


Figure 7-5. Core area cells used by group B.

Table 7-4. The surface distribution of five habitats types in the home range of the black gibbon group, the selectivity of each habitat by the gibbons over the study period.

Category	Area (and used) in home range (ha)	Annual occupancy records	Annual selectivity*	Core plots (26 ha) of the type all (%)
Habitat type				
Good valley	16(15)	738	2.1	50
Poor valley	30(26)	1124	2.17	43.3
Valley shrub	10(7)	83	1.7	10
Other shrub	26(19)	157	2.33	3.8
Good slope	6(6)	105	1.04	0
Total	88(73)	2207		100
Altitude (m)				
<2300	15(13)	1008	1.72	53.3
2300-2400	33(28)	793	1.99	33.3
2400-2500	39(31)	393	1.77	10.3
>2500	1(1)	13	1	0
Total	88(73)	2207		100

*Morista Index.

7.6.2. Seasonal Variation of Home Range Use

Black gibbons showed some marked seasonal variations in the patterns of home range use. **Figure** 7-5 illustrates the range size and the percentage occupancy per quadrat entered, based on all observations. **Table** 7-5 gives the number of quadrats entered and the degree of patchiness of occupancy during each month of the two years, and **Table** 7-6 for the same month pooled together. These results show no marked trends.

Comparing different periods of fruit productivity, range area was largest during the period of average ripe fruit supply (not total fruit) (from May to July), while the use of the range area was most uneven when fruit was extremely scare. In each observation case, I found that the high frequency of quadrat visits was concentrated on patches of some species with suitable foods. During June 1997, they mainly fed on *Myrica esculata*, and concentrated their time in plots d6,d7, d8 and c6 (a plot with shrubs, no tall trees).

But during May 1998, they stayed at d2,d4,d5, e5,e6,e7 and f5, because most trees (*Cerasus cerasiodes*) with ripe fruits were located in these plots (**Figure 7-6**). **Table 7-6** showed the plots used and the fruit availability index for three time period.

Table 7-5. The number of quadrats entered by the black gibbons (group B) and the Morisita's Index (I_δ) of the occupancy records during the two years.

Period	No. Quadrats entered	Moristat's I_δ
January 1997	14	1.95
February	7	2.27
March	21	4.33
April	10	1.72
May	24	2.00
June	15	2.16
July	5	1.91
August	9	1.17
September	16	1.13
October	18	1.67
November		
December	15	1.04
January 1998	16	1.92
February	26	1.94
March	25	1.85
April	1	
May	21	2.4
June	34	2.32
July	4	2.84
August	8	1.11
September	29	1.5

Table 7-6. The number of quadrats entered by the black gibbons (group B) and the Morisita's Index (I_δ) of the occupancy records during three periods of different fruit supplies

Period	No. Quadrats entered	Moristat's I_δ	Ripe fruit availability index[a]
1997			
Sept-Oct	23	1.357414	11172
1998			
Feb-Mar	36	2.434261	940
May-June	40	2.416749	8638.5

a, data from **Chapter 4**.

The data might be biased by uneven sampling: there is a significant correlation between the number of records and the number of plots they entered (**Figure 7-4**)

($r_s=0.824$, $n=20$, $P<0.001$). However, when we only compared three periods with most records: September to October (1997), February to March (1998) and May to June (1998), range area was still largest during the period of average ripe fruit supply from May to June, while the use of the range area was most uneven when fruit was extremely scarce in February to March period (**Table 7-6**). In both the first and third periods, the fruit abundance is high, but ripe fruit is more abundant in the September to October period, and total fruit is more abundant in the May-June period.

7.7. Ranging of Group B in the Two Study Periods (1989 *vs.* 1997-8)

Day journey lengths are similar for the two study periods (1989 *vs.* 1997-8), although group size is different. It is possible they can get enough food in the daily range area covered, so there is no need to exploit other parts of the home range. Most of their home range (sectors ‘a’ and ‘b’) is isolated from other groups’ habitat, and so there is almost no need to come into conflict with other groups for resources.

An alternative explanation is that travel costs do not, in fact, increase in direct proportion to group size. The feeding effort and travelling effort may not increase in large groups so long as the size of the group does not exceed the capacity of the resource patch it feeds on. In the Mangabey, group sizes as large as 12 to 15 (Waser 1977) or even larger (Barrett, 1995) do not seem to incur significant travel costs.

Nonetheless, the black gibbons might use more area as their home range as group size increased. As discussed above, during 1989, we can only confirm a few plots the group entered as our field observation time was limited, and I estimated their home range according to the forest available to the group (size, isolation and connection status). I proposed that they only use 2 or 3 sectors (‘a’, ‘b’ and ‘c’), but none of sectors ‘d’ and 'e'. The same 3 sectors are still the main home range area for the group in the present study period, but they also ranged out to sector 'd' and possibly other forest patches (*e.g.* sector 'e').

7.8. Ranging of Other Groups

The range size of group F and other groups can not be estimated accurately, because there are not enough data. Some authors have suggested that several groups ranged in the same area, with ranges that overlapped heavily. But based on forest availability and the calling and observational data, I have estimated this group's range size for comparison, nonetheless.

Group F's range area is about 208.5ha (in about total 231 1-ha plots). If the area assumed to be group G's range is excluded, the figure would be 140 ha. If we correct for slope, (average 26.5 degree of the slope), the area is 233 (156.4)ha. This is a very large range, even compared to that of group B. But the group might not really use all the areas, but just part of it.

In 1987-8, there were 2-3 groups (group F and D/E) and one single adult male (C). Jiang *et al.* (1994a) observed the group of more than 9 individuals twice, and later only 4 and 5 individuals each in the group suggesting that these might be two or more groups that sometimes come together. We have some records that group B's members can be far as 200 meters and in different valleys from each other. It is possible that I mistook a pair of adults of group D for another group (E) in 1988. But Sheeran (1993) and Jiang *et al.* (1994 a, b) believed that there was 5-6 groups: D/E (they named either C2 or CA, respectively) in south part of the Xiaobahe area, and F (CB or) and G in the middle parts of the area, and C3 and possible one other in the north part of the area

(Chapter 3). Despite this confusion, at least 3 groups (F,G, C3) should be real **(Chapter 3)**. During 1997 to 1998, in the previous home ranges of groups D/E, C and F, only group F was observed, with 5 individuals, since only one group was found there.

During 1987-1989 and possibly later in 1990, Group F and group D appeared to be two different groups since both the observation and singing data confirmed that two groups ranged in the area **(Chapter 3)**. In this case, the size of group F's range should be about half that estimated above. Moreover, in the most recent studies, group F has not been observed ranging in all the area that we suppose to be their home range. These analyses suggest that the real home range size of group F might be similar to or only slightly bigger than that of group B.

7.9. Rodman & Mitani's Index

The Rodman-Mitani index (Mitani and Rodman, 1979) is a good index to measure territoriality in primates. Here we calculate the indices and list them in **Table 7-7**. We can see, from the data provided by Chen (1995), that the black gibbon could be territorial. However, the data provided by both my previous study and the present study yield an index that suggests that the black gibbons will only have weak territoriality at best.

Table 7-7. Ranging behaviour and Mitani-Rodman index based on home range size in black gibbon groups*

Group code	Home range	Day journey length	Rodman & and Mitani index	Source
AC2	87	1306	1.24	Chen (1995),
B	49	795	1.006	Lan (1989)
B	49.1	838	1.0596	Present study
Hainan	362.5	?	0.057	Liu *et al*(1989), Sear (1994)

*For the group from Hainan, no information on day journey length was given, so the mean day journey length for the black gibbons was used.

Figure 7-6. Map shows the habitat of group F and its ranging.

In sum, the index shows that this species is capable of being territorial, but only weakly so. This conclusion agrees well with observations which suggest that black gibbons are less actively territorial than other gibbon species. Only one territorial encounter was observed (Sheeran, 1993), and singing is relatively rare (*e.g.* compared with hoolock, black gibbons showed low frequency and short duration in their morning song, Lan *et al.*, 1999, and unpublished data) even though interactions did occur. Some observations suggested that the encounters between groups can be peaceful (Jiang, 1994c) and some groups might experience fission and fusion, or at least new group formation might occur through splitting (Jiang *et al.*, 1994c; Liu *et al.*, 1984). I have observed that group B members ranged widely sometimes. So from this point of view, some groups I counted between 1987 to 1989 are possibly just part of a bigger group, especially the 'group E' within the home range area of group D. But group D was a different group to the group F, since their compositions are different. More over, we heard them calling to each other near my camp site. One day morning (24 May, 1997), 23 minutes after group B heard the calling of group F, group B called and travelld towards group F.

If day journey length is influenced by patrolling behaviour it is to be expected that territory size may relate to day journey length in some way. This does not appear to be the case in hylobatids. When the Mitani-Rodman defendability index is calculated for these gibbons, both territory and home range size seem to be defendable, and it seems even the shortest gibbon day journey length is long enough to maintain sufficient guard over the territory.(Sear, 1994). However, if the modified version of Lowen and Dunbar (1994) is used the territories of the *H. pileatus* group in Thailand and the *H. muelleri* in Kalimantan (six home ranges) do not appear to be defendable (0.071 for *pileatus* and 0.06 for *muelleri*, less than 0.08, Appendix 1, Sear, 1994). This modification equation is more complex than the Mitani-Rodman index and it may be that its assumptions do not always hold true for hylobatids. It should be noted that one of these additional variables is the detectability distance of intruders and the standard figure (50m) used by these authors may be slightly high for forested environments; if detectablity distance is reduced this will decrease the likelihood of hylobatids being able to defend their ranges. One factor neither index takes into account is population density, and it may be that low population density allows hylobatids to occupy territories they would be unable to defend if the environment were at carrying capacity (Sear, 1994)

7.10. Summary

In this chapter, I have discussed the ranging behaviour of group B. The day journey length and home range size in this group are not very unusual. Although home range size is large by compares with other hylobatids, it is perhaps not as large as some earlier studies proposed. Their day range length is shorter than most gibbon species, but similar to that of siamang. They show that they do not have strong territorial interactions, and this might be caused by the low group density. When fruit is abundant, they showed much longer ranging distances and bigger ranging areas. They also showed that they do not use the home range evenly, but patchily, depending on the resources availability. Their best choice is the plots with good forest and edge, possibly convenience for both food exploitation (in the edge part) and safety (in dense forest canopy).

CHAPTER 8. COMPARISON BETWEEN HYLOBATIDS

8.1. Introduction

Previous attempts to describe the behaviour of primate groups in terms of environmental and other behavioural variables have met with good success (gelada: Dunbar 1992a; baboons: Dunbar, 1992b; Hanuman langurs: Srivastava and Dunbar, 1997; chimpanzee: Williamson and Dunbar, 1999). Based on previous efforts by Sear (1994), a similar analysis is carried out here on hylobatids (Genus, *Hylobates*), a primate species group occupying a different habitat to those already studied, *i.e.* an arboreal forest rather than terrestrial open country. In next chapter social system models will be examined. I will discuss the data set (**8.2**), then I will present differences between gibbons and siamang (**8.3**), and differences between black gibbons and other allopatric gibbons (**8.4**); hoolock gibbons and black gibbons (**8.5**); Allopatric and sympatiric gibbons (**8.6**). Finally I will give a short discussion and summary (**8.7**).

8.2. Data Set

The data set was originally compiled by G. Cowlishaw and a preliminary analysis of correlation between variables was undertaken by Sear (1994). The data set was augmented by data on black gibbons from the present study. Including data from this study, the data derive from twenty- three studies at fifteen sites (**Appendix 2**). Locations are widely distributed across the gibbon's range but they are not evenly distributed (Sear, 1994). Sear (1994) gives a very detailed discussion of the variables selected for the data set. Here I just point out some important points.

In this data set, nine hylobatid species are represented. All 23 studies give at least some data on environmental and population variables (*e.g.* population density and biomass), and territorial behaviours; nineteen give data on time budgets, and seventeen on diet and day journey length. Although most studies were of reasonable duration, data are not of similar systematic quality. These studies were included because they might be either the only suitable study available of the species, or in order to balance the data set for geographic location.

8.2.1. Environmental Variables

A number of environmental variables were included since they have been shown to be relevant in other primates (Dunbar, 1993, 1992). Latitude and altitude are related to climate which affects forest structure and thus habitat quality. Latitude is also related to seasonality; as the distance from the equator increases, the seasons become more pronounced (Whitmore, 1984). This will affect the temporal distribution of food, a factor which affects many aspects of gibbon behaviour. Two other indices of seasonality were included in the analysis: temperature variation (calculated by subtracting minimum from maximum temperature) and an index of rainfall diversity ($Z=1-\Sigma_i P_i^2$, where P_i is the proportion of rain that falls in the *i*th month: Dunbar, 1992).

Rainfall and temperature both affect gibbon behaviour directly. Temperature affects energy requirements (*e.g.*, Caraco, 1979) and gibbons seem to dislike rain and frequently cease activity during heavy rainfall (Raemaekers, 1980). Both variables are also used as measures of productivity (Murphy, 1975; Rosenzweig 1968) and plant species diversity (Deshmukh, 1975; Hall and Swaine 1976). Minimum and maximum temperatures are included in analysis, as they might affect thermoregulation. All climatic variables (except temperature variation) included in the analysis are annual means.

The only direct information on food abundance in the data set is the number of fig tree density (stems per hectare). Figs are an important food source of gibbons because of their commonness and unusual life-history characteristics (Gittins and Raemaekers, 1980). Figs frequently fruit asynchronously both between and within species; they may also fruit at several times throughout the year, and may therefore provide a constant supply of figs (Leighton and Leighton, 1983). Further, they are found in large patches and tend to fruit over a larger proportion of their crowns than other plants (Raemaekers, 1979). It has been hypothesized that figs may be a keystone resource (Leighton and Leighton, 1983), *i.e.* a constantly available resource that allow animals with fixed ranges to survive through periods of food shortage, so the abundance of this type of food may have an importance to gibbons out of proportion to its abundance in the forest as a whole. However, some gibbons populations seem to survive perfectly well in areas where fig trees are scarce (*H. klossii* on the Mentawai islands, Tenaza, 1975; Tilson 1981), or absent (*H. concolor* at Xujiaba, Chen, 1995). Unfortunately, data on fig tree density is not complete.

Competition (for food and other resources) is a possible important factor affecting habitat quality for gibbons, and so the biomass and number of sympatric primate species in the study area are used in the analysis (diurnal species only). Non-primate species which compete with hylobatids are impossible to quantify now, and it was assumed that the more closely related primate species would be the major competitors, so other non-primate competitors have not been included in the analysis.

8.2.2. Population and Behavioural Ecological Variables

The next set of variables relate to population characteristics, group size, biomass, and density, etc., and behavioural ecology variables. These variables are expected to be affected by environment and will also influence each other. Two measures of the proportions of food types in the diet are included: the percentage of the activity period devoted to a particular food category and the number of minutes spent eating each food type. The amount of fruit in the diet was broken down into figs and non-fig fruit.

In some cases, some data are not available to use here, such as territory size in black gibbons. Home range size is available, but some of them seems implausible, such as that in Hainan black gibbons (Liu et at., 1989) and in hoolock gibbons (Mukherjee, 1986) whose groups ranged over a large area (ten times larger than the ranges of other populations). The populations did not appear to defend their ranges: Mukherjee's gibbon sang rarely except when other groups were nearby. Liu *et al* (1989) give no information on singing but state that intergroup conflicts were rare. It seems then, that these populations, and possibly all black gibbon populations, were living at such low density that they did not need to defend territory but are more free to occupy unusually large tracts of land. The use of the Mitani-Rodman (1979) defendability index (and its modification by Lowen and Dunbar, 1994) suggests that these two group (Liu's concolor and Mukherjee' hoolock) could not physically defend such large territories (Sear, 1994) (**Chapter** 7). In order to control for the effects of group size and body weight, territory and home range size were included in the analysis as territory/home range size per kilogram as well as in absolute terms.

Predation risk was not included in the analysis as it has to be fairly low to allow gibbons to live in small groups, although this does not mean that it is non-existent. Hylobatids display alarm call at potential predators such as raptors and humans (*e.g.* Chivers, 1977; Jiang *et al.*, 1994c; personal observation). It seems that some populations may suffer particularly badly from human hunting *e.g.* kloss gibbons on Siberut (Tenaza and Tilson, 1985), and black gibbons in Yunnan 10 years ago (Lan, 1995b).

8.3. Differences between Gibbons and Siamangs

8.3.1. Diet

The **Table 8-1** shows that results of the statistical analysis (Kruskal Wallis H test) of the differences between gibbons and siamang. The behavioural ecology of these two groups have been shown to differ when populations occurring in the same habitat (*e.g.* MacKinnon, 1977; Raemaekers, 1979).

The siamang are not more folivorous than most gibbons as obvious as previous analyses have suggested (Sear, 1997). This might be due to the highly folivorous diet of the black gibbons and some recent more frugivorous siamang cases (Palombit, 1997) included in the analysis. If the data for black gibbons are removed, the difference is significant (X^2=6.82 , P=0.009). The amount of time that siamang devote to feeding on figs is not significantly different to that for gibbons, but on non-figs is (X^2=5.88, P=0.015). Raemakeres (1979) suggested that siamang consume figs at a slightly slower rate than lars, but when all types of fruit are considered the consumption rate does not differ between these two species (Raemaekers, 1979; Chivers and Raemaekers, 1986). Recent publications confirm that siamang may obtain a relatively high portion of figs where the figs are available (Palombit, 1997).

No significant differences are found between the number of minutes siamang spend eating fruit, suggesting that they consume approximately the same absolute quantities of fruit as gibbons despite their larger size. However, when the faster ingestion rate and longer time devoted to leaves are taken into account, siamang's proportion of the caloric intake supplied by leaves is probably substantially higher than gibbons'.

Table 8-1. The differences between siamang and gibbons.

Category	Gibbon median	Simang median	Kruskal-Wallis H	P
Fig trees (n/ha)	2.1	10.4	1.738	0.187
Population density (n/km^2)	7.75	8.55	0.223	0.637
Group density (gp/km^2)	2.1	2.15	0.223	0.636
Group size	3.6	3.95	0.369	0.529
Biomass	32.6	67.85	1.75	0.186
Encounter per day	0.08	0	1.08	0.289
Song bouts per day	0.6	0.27	5.34	**0.021**
Territory (ha)	28.2	16	1.4	0.237
Relative territory (ha/kg)	1.9	0.5	5.66	**0.017**
Home range (ha)	44	27.6	2.89	0.089
Relative home range (ha/kg)	2.6	0.8	8.13	**0.004**
Overlap (%)	19.5	20	0.28	0.598
Activity period (minutes)	550	615.5	4.21	**0.04**
Day journey (m)	1250	774	3.71	0.054
Time budget				
Feed (%)	39	51.5	2.26	0.133
Travel (%)	21	16	1.14	0.287
Rest (%)	33.9	29	0.059	0.808
Sing (%)	3.5		4.15	**0.042**
Social (%)	5.6	2.5	2.75	0.097
All fruits (%) in diet	60.5	43	2.6	0.107
Non-fig fruit (%)	38.25	18	5.88	**0.015**
Fig (%)	25	22	0.07	0.792
Leaves (%)	31	43	1.75	0.186
Flowers (%)	5.25	6	0.14	0.708
Arthropods (%)	2	8.5	0.985	0.321
All fruit (minutes)	112	122.5	0.013	0.91
Non-fig fruits (minutes)	63	42.15	0.857	0.355
Fig (minutes)	48	64.5	1.93	0.165
Leaves (minutes)	65	147	2.17	0.141

8.3.2. Time Budgets, Day Journey Length

Time budgets appear to differ little between gibbons and siamang. Siamang spend a slightly shorter part of their activity period moving (but without significance) than gibbons, and their day journey length is almost significantly shorter than that of gibbons ($H=3.7$, $P=0.054$). It is possible that siamang's slower movement cause the shorter day journey length. Raemaekers (1979) calculated that siamang only travel 0.6 times as fast as lar gibbons.

In contrast to other folivorous primates, siamang do not spend more time resting and less time feeding than gibbons. Leaf-digesting is a time consuming and energetically expensive process, and this can only be done while resting. The difference in siamang may have something to do with its heavier body weight, and the similarity in feeding rates to the gibbons. If siamang eat about the same quantities of fruit as gibbons in about the same time, then they need to consume a considerably larger amount of leaves in order to fulfil their absolutely greater metabolic needs. This specific diet niche difference (folivory) might require that siamang spend longer feeding in both absolute terms and as a proportion of their activity budget.

These results also confirm previous findings that siamang seem to expend less energy on maintaining their territories (*e.g.* Chivers, 1974; Rijksen, 1978, by Sear, 1994). They sing significantly less frequently than gibbons ($X^2=5.343$, $P=0.021$) (encounter rate is also lower but this result is not significant), and they do seem to spend a significantly shorter proportion of their active period singing ($X^2=4.152$, $P=0.042$). This may relate in some way to their smaller range sizes (folivorous primates tend to have smaller ranges than frugivous species: Clutton-Brock and Harvey, 1977) but not significantly higher population density, so that they may have fewer territorial neighbours than gibbons.

The territory and home range sizes of the siamang are not significantly smaller in absolute terms, but when biomass is taken into account (*i.e.* when territory/ home range sizes per kilogram are compared) the differences in both variables become significant (territory:

$X^2=5.662$, $P=0.017$; home range: $X^2=8.13$, $P=0.004$).

These results suggest that siamang do have some species-specific characteristics not shared by gibbons. However, no siamang population which lives apart from any other hylobatid species is included in the analysis, so the situation should be much more complicated. There are indications that siamang are more frugivorous when they do not suffer from competition from gibbons or in habitats with abundant fruits (Palombit, 1997). It is reasonable that smaller, more scattered fruit sources should be less profitable for the larger siamang whether or not they have to compete with gibbons. However, without sufficient quantitative data this can clearly be only speculation, but fig density may be particularly important to siamang, at least when they are in sympatry with gibbons. Figs are more numerous at sites where siamang and gibbons do coexist than where they do not. This relationship does not achieve statistical significance, but it may be meaningful that siamang and the gibbons they are sympatric with are able to maintain similar proportions of figs in their diets to other gibbons populations (except black gibbons) who live without the competition of another hylobatid. Hence, it may be that the density of figs is the key to the coexistence of such similar primates.

Examining the differences between gibbons and siamang in terms of the proportions of fruit and leaves in their diets may underestimate the contrasts between the feeding behaviour of these two groups. Within the broad categories of fruit and leaves siamang and gibbons may be feeding on different species of plants or on different plant parts. Although the species composition of their diets does seem broadly similar (MacKinnon, 1977), it has been observed that siamang feed on more mature leaves than lar gibbons (though they are still restricted to young leaves) and Rijksen (1978, by Sear, 1994) has also noted that gibbons appear more selective than siamang when feeding on figs. This will further reduce competition between gibbons and siamang in sympatry.

8.4. Differences Between Black Gibbons and Other Allopatric Gibbons

8.4.1. Diet

The **Table 8-2** shows the results of the statistical analysis of the differences between black gibbons and other allopatric gibbons.

The black gibbon groups are significantly more folivorous than other gibbon groups; they also consumed significantly smaller quantities of all types of fruit than the other gibbons. The proportion of their active day that black gibbons devote to figs is significantly less. As reported by Chen (1995), the black gibbon groups in some habitat will have no figs at all in their diet because no figs at all. So it is clear that the black gibbons, in this way similar to siamang, rely heavily on leaves for energy.

No significant differences are found between the number of minutes black and other gibbons spent eating non-fig fruits, suggesting that they may consume approximately the same absolute quantities of time to search fruit as other gibbons assuming that intake rates do not vary between the species. We do not have evidence to support the claim that black gibbons spend significantly more minutes per day eating leaves than other gibbons, although the time proportion spent on leaves is of significance.

The black gibbons may be likely to consume fewer arthropods, partly because the limited availability of these, and feeding on arthropods might not provide a good return on the amount of energy needed to catch them. It may be that black gibbons obtain sufficient protein through consuming larger quantities of leaves like siamangs. However, there is no significant difference between the groups in the time devoted to arthropods.

Table 8-2. The differences between black gibbons and other allopatric gibbon species.

Category	Allopatric gibbon median	Black gibbon median	Kruskal-Wallis H	P
Fig trees (n/ha)	2.05	1.5	2.036	0.154
Population density (n/km^2)	9	1.73	4.667	**0.031**
Group density (gp/km^2)	3	0.43	4.680	**0.031**
Group size	3.3	4.15	1.303	0.254
Biomass	49.9	17.05	4.667	**0.031**
Encounter per day	0.008?		2.423	0.12
Song bouts per day	0.73	0.4150	2.470	0.116
Territory (ha)	27			
Relative territory (ha/kg)	1.9			
Home range (ha)	35.5	71	4.875	**0.027**
Relative home range (ha/kg)	2.45	4.25	1.413	0.234
Overlap (%)	24			
Activity period (minutes)	565.5	509	0.667	0.414
Day journey (m)	1100	838.7	0.636	0.425
Time budget				
Feed (%)	41	33	1.444	0.229
Travel (%)	18	22	0.168	0.682
Rest (%)	29	39	1.052	0.305
Sing (%)	4	3	0.656	0.418
Social (%)	7	5.6	0.125	0.724
All fruits (%) in diet	62	24	5.361	**0.021**
Non-fig fruit (%)	43	24	4.267	**0.039**
Fig (%)	26	2.3	5.445	**0.020**
Leaves (%)	28	54	6.231	**0.013**
Flowers (%)	4.5	6	0.377	0.539
Arthropods (%)	1	?		
All fruit (minutes)	123	39.2	5.727	**0.017**
Non-fig fruits (minutes)	95.5	24.7	3.125	0.077
Fig (minutes)	49	4	4.5	**0.034**
Leaves (minutes)	64	89	0.325	0.569

No significant group size differences are presented here, as the data are limited. Some data suggesting bigger group sizes (Haimoff *et al.*, 1986; Jiang *et al*, 1994a, b) are not included in this analysis since no other data available. Nonetheless, it is clear that mean group size for this species are typical, but possible larger than other species (**Chapter 3**).

8.4.2. Time Budgets, Day Journey Length:

Time budgets appear to differ little between black gibbons and other gibbons. Black gibbons' day journey length is not shorter than that of other gibbons if all available data are considered. However, if only my data on group B are included in the analysis, the difference would be significant. Other gibbons do spend a slightly longer part of their activity period moving but this difference is not significant.

These results might support the ideas that black gibbons seem to spend less energy on maintaining their territories (Lan, 1989). The home range sizes of the black gibbons are significantly larger, but maybe only in absolute terms (Home range: X^2=4.875, P=0.027). Given that black gibbons tend to live in larger territories it is to be expected that they would occur at low densities than other gibbons. So it is also reasonable to expect that encounter rates between groups in black gibbons are low, as suggested by the field data (See Sheeran, 1993).

These results suggest that black gibbons have some species-specific characteristics not shared by other gibbons. There are indications that black gibbons may be more frugivorous when they live in better habitats with abundant fruit (Liu *et al.*, 1989, Liu and Tan, 1990). But their flexibility in feeding adaptation are possibly related to their other adaptations, such as an occasionally polygynous social system (**Chapter 3**).

8.5. Hoolock gibbon and Black gibbons

Both hoolock and black gibbons represent the most northerly distributed gibbon species, and they may show some specific adaptations to colder habitats. Sear's (1994) analysis showed that there are no differences between hoolock and other allopatric gibbons (not include black gibbons). When hoolock and concolor together compared with other allopatric gibbons, some categories did differ significantly (**Table 8-3**), but most do not. The most obvious differences lies in population density (as well as group density and biomass). This might imply that the habitat in northerly ranges show some decline in density and so cannot support high biomasses. Home ranges are also different, but this might be due mainly caused by black gibbon data, since except one high estimate by Mukherjee (1986), other data for hoolock are similar to other gibbons. There are no clear difference between black and hoolock gibbons even though both species live in northerly ranges.

8.6. Differences Between Allopatric *vs.* Sympatric Gibbons

The difference between allopatric and sympatric gibbon populations are shown in **Table 8-4**. Except in respect of fig tree density and the time spend in social activities, there are no significant differences between them.

Table 8-3. The differences between black - hoolock gibbons and other allopatric gibbon species.

Category	Median (black and hoolock)	Median (allopatric gibbon)	Kruskal-Wallis H	P
Fig trees (n/ha)	1.5	2.05	2.036	0.154
Population density (n/km^2)	1.725	10.2	6.612	**0.01**
Group density (gp/km^2)	0.425	3	6.267	**0.012**
Group size	3.2	3.4	0.702	0.402
Biomass	17.05	45.9	5.898	**0.015**
Encounter per day	0	0.08	2.423	0.12
Song bouts per day	0.43	0.6	0.327	0.568
Territory (ha)	31.5	22	2.143	0.143
Relative territory (ha/kg)	2.05	1.5	1.059	0.303
Home range (ha)	71	32.5	5.769	**0.016**
Relative home range (ha/kg)	4.25	2.2	3.103	0.078
Overlap (%)	?	24	1.018	0.313
Activity period (minutes)	540	567	0.3	0.584
Day journey (m)	838.7	1335	2.455	0.117
Time budget				
Feed (%)	36.5	35	0.026	0.873
Travel (%)	22	18	0.210	0.647
Rest (%)	30.8	37	0.098	0.754
Sing (%)	3	4	1.62	0.203
Social (%)	6	6	0.600	0.439
All fruits (%) in diet	40.4	62	1.647	0.199
Non-fig fruit (%)	38.5	43	0.960	0.327
Fig (%)	7.4	25	0.741	0.389
Leaves (%)	51.2	30	1.641	0.2
Flowers (%)	6	3.5	1.415	0.234
Arthropods (%)	7	1.5	0	1
All fruit (minutes)	70	123	1.844	0.175
Non-fig fruits (minutes)	45.35	76	1.125	0.289
Fig (minutes)	9.25	48	1.125	0.289
Leaves (minutes)	89	64	0.011	0.917

Table 8-4. The differences between sympatric and allopatric gibbons.

Category	Sympatric gibbon median	Allopatric gibbon Median	Kruskal-Wallis H	P
Fig trees (n/ha)	10.4	1. 5	7.064	**0.008**
Population density (n/km^2)	7.2	8.3	0.005	0.946
Group density (gp/km^2)	1.8	2.5	0.222	0.637
Group size	4.1	3.35	2.314	0.128
Biomass	29.5	3.6	0.222	0.638
Encounter per day	0	0.08	0.450	0.502
Song bouts per day	0.575	0.6	0.185	0.667
Territory (ha)		27	1.485	0.223
Relative territory (ha/kg)		1.9	0.031	0.86
Home range (ha)	55	41.5	0.631	0.427
Relative home range (ha/kg)	3.3	2.55	0.333	0.564
Overlap (%)	?	24	0.048	0.826
Activity period (minutes)	553	550	0.17	0.896
Day journey (m)	1521	975	2.857	0.091
Time budget				
Feed (%)	42	36.5	0.256	0.613
Travel (%)	32	20	1.565	0.211
Rest (%)	32.5	33.9	0.012	0.914
Sing (%)	?	4	0.429	0.513
Social (%)	2.5	6	4.200	**0.040**
All fruits (%) in diet	58	61.5	0.033	0.855
Non-fig fruit (%)	28	39	1.923	0.166
Fig (%)	26	24	1.049	0.306
Leaves (%)	29.5	35	0.941	0.332
Flowers (%)	1	5.5	0.884	0.347
Arthropods (%)	3	1.5	2.729	0.099
All fruit (minutes)	130	106.5	0.714	0.398
Non-fig fruits (minutes)	56.85	66	0.343	0.558
Fig (minutes)	68.35	33	2.143	0.143
Leaves (minutes)	65	76.5	0.716	0.397

8.7. Discussion and Summary

In this chapter, I have reviewed the available data on hylobatid behavioural ecology. The differences between the various species do not seem to be as prominent as previous studies have suggested. The most important differences are between the siamang and the other gibbons, and most of these can be explained in terms of differences in body size. The next most important differences seem to reflect the extreme habitat quality and larger body weight of black gibbons (and in some cases including hoolock gibbons).

Gibbon time budgets in general follow the trends typical for other primates species. Since gibbon habitats does not seem to be impoverished, we are led to ask why they do not live in large groups, as the other primates do? To what extent are their group sizes limited by their habitat carrying capacity? We will try to answer these question in next chapter.

CHAPTER 9. MODEL OF THE GIBBON SOCIO-ECOLOGICAL SYSTEM

9.1. Introduction

In the previous chapter, I discussed the difference between hylobatid species, especially siamang/black gibbons and other gibbons. Here I present and test two social-ecological models for all hylobatids. First, regression analysis is used to establish the equations between the main variables, then these equations are built into the general primate social ecological system model developed by Dunbar (1992a, 1996). The original model was constructed for baboons and extended to chimpanzees by Williamson and Dunbar (1998). Although simple, these models have turned out to be surprisingly good at predicting both maximum group size and the geographic distribution of these species.

Here two models are presented: one is a time constraint model based on the time budget (Model I). The other is an resource constraint model on the basis of biomass or habitat carrying capacity (Model II). Model I predicts the ecological tolerable maximum group size; Model II determines the mean group size (Biomass constrained group size) as determined by food availability and quality. The models were built by R. Dunbar, on the basis of equations obtained by me. I then tested the models and explored their implications.

9.2. Sources of Error

As pointed by Sear (1994), some of the climatic data were taken from long-term studies of climate at nearby sites, in order to increase the data set. Climatic variables such as temperature and rainfall taken from the studies themselves will clearly only describe the weather conditions at the time of the study. Given that behaviour is likely to track short term changes in environment (*e.g.* day journey length: Raemaekers, 1980), these variables are expected to show closer correlation with behaviour than long term averages and the use of long-term averages may adversely affect the results.

Using data from numerous studies in this way will introduce some error due to methodological differences. However, this should introduce error variance which will tend to reduce the significance of the results leading to false negatives rather than false positives (Cowlishaw, 1992). The category which may suffer the most from these differences in methodology is that of time budgets because of differences in the definitions of categories used between observers. The data in this category show considerable variation (this may of course be due to environmental variables rather than methodological differences) but the proportion of time spent feeding varies eight-fold (8-67%); in addition, most studies give information on time spent feeding, moving, and resting, but few do so on time spent singing or in social behaviour. When the foraging category is used, feeding time is calculated by adding the time spent in feeding bouts to 50% of the time spent foraging. The percentage of time spent moving is also therefore 50% of foraging time added to the time spent solely in travelling.

Another factor which might affect the comparability of the data is that, while data on variables such as group and territory size are frequently population means, data on time budgets and diet are typically based on just one or two groups of animals. This will create anomalous results if the group or individuals within it are not representative of the population as a whole: the likelihood of this may be increased because study groups are often chosen from the edge of a population, where habitat may be of poorer quality, *e.g.* because of human disturbance, but with better observation condition.

9.3. Time Budget Model

9.3.1. What Does the Model Do?

We assumed that the maximum Ecological tolerable group size (N_{max}) can be determined by the amount of time gibbons can afford to devote to social activity (as in the baboons, grooming is the main factor which keeps the group members together), giving the habitat-specific climatically determined requirements for feeding, travelling and resting. In this context, resting time is the minimum time that the habitat forces the animals to spend resting. This component of resting time appears to be time out that the animals cannot use for any other purpose (including social interaction). However, it is unlikely that all resting time is of this kind: in more equitable habitats, at least part of it will be spare time that is not currently needed for any other purpose.

9.3.2. Constructing Model

Using the data set of **Appendix 2**, correlation and regression analysis were carried out in order to establish the relationship between variables and then reduce the variables to the two main independent climatic variables (Temperature and rainfall). Derived variables, such as rainfall diversity (Z) and temperature variation, are used to describe habitat use, population parameters and behaviour. Based on those relations, we obtain a diagram which describes the relationship between variables (**Figure 9-1**).

Only two variables (temperature, rainfall) are not determined by other variables, but are the driving variables of the system. Some variables, like altitude and latitude, are not determined by temperature and rainfall naturally, but we assume they can be predicted by given temperature and/or rainfall, in order to reduce the number of independent variables to just temperature and rainfall, and to be able to present the results in two dimensions on the page.

Equations used in the model were determined either by stepwise regression or by ordinary linear multiple regression where stepwise procedures produced poor or biologically unconvincing equations. The aim was to find equations describing key variables in terms of particular independent variables so as to make the model coherent and self-consistent. In other words, the chain of equations had to lead back to just two driving climate variables (rainfall and temperature). To do this, the bivariate plots of dependent variable against a number of possible independent variables (with these being chosen partly on grounds of biological plausability – *i.e.* those variables that seemed likely to influence the dependent variable on biological grounds) were examined. Then, all these variables were put into a multivariate regression equation and the partial significance of each variable in the regression table examined (**Table 9-1**). Next we reran the regression omitting those variables that seemed to have little effect on the dependent variable when interacting with other independent variables. This allowed us to remove variables that were not influencing the dependent variable independently. As in the baboon model, independent variables were included in some cases even if their partial regressions were not individually significant providing that they added a large amount to the r^2 value (*e.g.* their inclusion increased the amount of variance explained by about 10%).

In order to determine the maximum group size that the animals could tolerate without placing excessive stress on their time budgets, a simulation procedure was used to find the largest group size at which all available time was allocated to the four main time budget components (feeding, travelling, resting, and social time). This is done by increasing group size progressively until all the spare resting time initially available has been converted into feeding, travelling, and social time.

Table 9-1. Regression equations for the hylobatids time budget model.

Equations	R^2	P value
LLAT=9.362001-2.374*LOG(T)	0.525	P<0.001
LALT=19.392-3.583*LOG(T)-0.331*LOG(P)	0.680	P<0.001
LBMS=4.252-0.438*LLAT	0.227	P=0.034
LMAXT=1.825+0.05*LLAT+0.506*LOG(T)	0.886	P<0.001
LACT=4.57+0.2294*LOG(P)	0.352	P=0.009
LTV=2.397+0.296*LLAT	0.747	P<0.001
TV=40.444-0.862*T	0.654	P<0.001
Z=0.9781-0.0047*TV	0.887	P<0.0001
LFT=-11.173+2.082*LOG(P)-0.602*LALT	0.80	P<0.0001
LBW=0.917+0.084*LOG(P)-1.616*LOG(H)-0.016*LFT	1	P<0.001
JL=6.155+0.654*LOG(N)	0.111	P=0.266
LHR=6.0505-0.6565*LBMS	0.591	P<0.001
FL=O.206+0.642*LOG(T)-0.224*LOG(P)+1.714*LBW	0.726	P=0.012
FL=3.767-0.330LOG(P)+0.455LOG(T)+0.521LBW	0.73	P<0.001
ML=-0.8614001+0.694*JL+O.42*LHR+0.834*LACT	0.424	P=0.123
S=4.5332+0.0764*N		
RL=8.379-0.27*LLAT+0.464*LOG(P)-2.3*LMAXT	0.933	P<0.001

Notes: Variable names in the programmes in the model:

T=mean annual temperature
P=total annual rainfall
Z=rainfall evenness
LAT=latitude
ALT=altitude
BMS=biomass
ACT=length of activity period
TV=temperature variation
FT=fig tree density
BW=body weight
LFIG=loge of proportion of figs in the diet
LLP=loge of proportion of leaves in diet
J=day journey length
FL=loge of time spent feeding (%)
ML=loge of time spent travelling(%)
RL=loge of time spent resting(%)
SL=loge of time spent social (%)
HR=home range size
LGDEN=loge group density
POP=population size (number of animals)

LLAT=loge **LATITUDE**
LALT=loge **ALT**
LBMS= loge **BMS**
LACT=loge **ACT**
LTV=loge **TV**
LFT=loge **FT**
LBW=loge **BW**
JL=loge **J**
LHR=loge home range

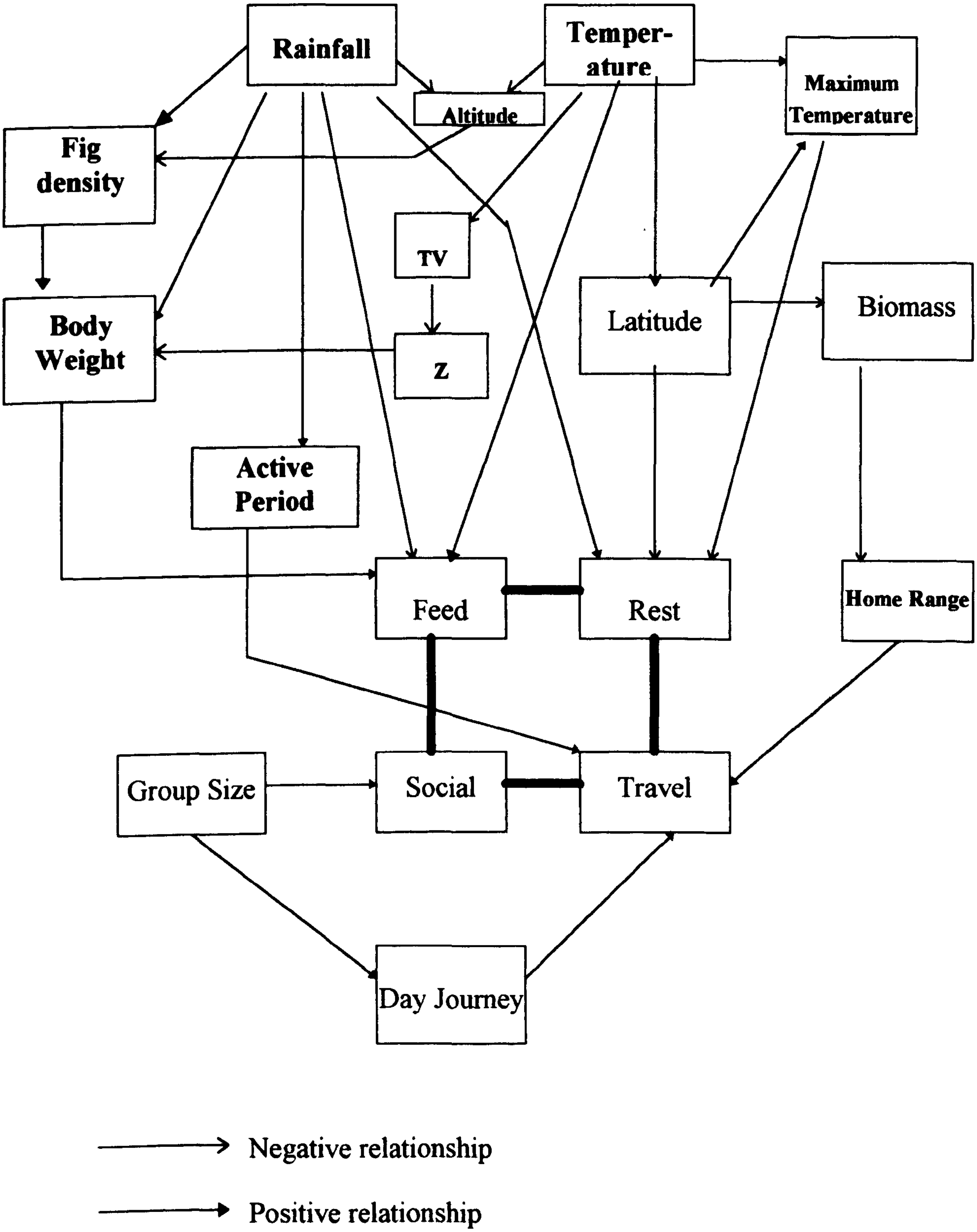


Figure 9-1. Flow diagram for time budget model used to predict maximum ecological tolerable group size.

Model I seeks to determine how time budgets limit group size. This model imposes some constraints:

> **Rainfall diversity (Z)** cannot be larger than 0.9167 (this is a mathematical fact); if the equation for Z yields a value larger that this, then Z is assumed to be 0.9167.
>
> **Resting time (R)** cannot be less than 5% (animals must spend some time resting and/or changing between other activities).
>
> **Body weight (BW)** cannot be larger than 12 kg or smaller than 4 kg; If **BW** exceeds these limits, then **BW** is taken to be 0 and the animals cannot live in the habitat.

All equations except that for social time were obtained from the hylobatid (either with or without siamang) data base. For non-environmental variables, siamang data were excluded from the analysis because their diet is more folivorous than that of other hylobatids. The social time equation is the only equation not obtained from the hylobatids data base, because it is not possible to get one according to the regression (usually the social time in gibbons are too small in proportion of time budget). Since we know that the social time required are mainly determined by social environment, like interaction numbers between social members, we assumed that the social time are determind by the group size as in other Old World primates. So the equation for social time is the same as that used in all the time budget models and is based on the relationship between group size and grooming time in Old World monkeys and apes (**Table 9-1**) (Dunbar, 1993).

9.3.3. Results

Table 9-2 shows how maximum ecological tolerable group size varied with annual temperature and rainfall. The results in **Figure 9-2** show that the lower the rainfall, the bigger the group size. The largest group sizes occur in habitats with higher temperature and low rainfall. The results suggest that the gibbons can live in habitats of low rainfall well, even if it is quite cold (around 5 °C or lower ---close to freezing point).

It is difficult to explain why group size should be bigger in low rainfall habitats but not in the high rainfall habitat. Raemaekers (1980) suggested that the gibbons usually stop activity when the rain comes suggest that rain interfere the gibbons' social interactions. I have observed that black gibbons stop activity including grooming when rain becomes heavier (unpublished data). However, rainfall must have something to do with the growing conditions of preferred plant species (*e.g.* figs, lianas) especially food species. Although most tree species grow better in wetter habitats, it may be that very wet habitats may negatively affect growth rates, and so cannot support high gibbon density compared with drier habitats that are not short of water (mountain riverbed, foggy forest). In these high rainfall areas, group sizes are lower.

If we analyse the feeding proportion required by the model (**Table 9-3, Figure 9-3**), we find that the higher the temperature, the more time is required for feeding, especially in low rainfall habitats. The average feeding time in the sample populations is between 20-40%. The rapid decline of feeding time in low temperature habitats is puzzling. It is not clear whether this reflects an inadequacy in the model (extrapolating beyond the limits of the data base) or a genuine biological effect. The low feeding time requirements when temperature is at 0°C seems biologically implausible: most species increase feeding time as temperatures fall. However, it remains the case that hylobatids are found in habitats of temperature range 5 to 35 °C, and rainfall 500 mm to 4500 mm (**Appendix 2**).

Table 9-2. The maximum ecological tolerable group size for gibbon habitat

		Annual temperature (℃)							
		0	5	10	15	20	25	30	35
Rainfall	100	4	35	36	34	31	30	29	25
(mm)	500	0	15	18	19	19	20	21	19
	900	0	9	12	13	14	15	16	15
	1300	0	6	9	10	11	12	12	12
	1700	0	5	7	8	9	9	10	10
	2100	0	3	5	6	7	8	8	8
	2500	0	2	4	5	6	6	7	7
	2900	0	2	3	4	5	5	6	6
	3300	0	1	2	3	4	5	5	5
	3700	0	1	2	3	3	4	4	4
	4100	0	1	2	2	3	3	4	4
	4500	0	0	1	2	2	3	3	3

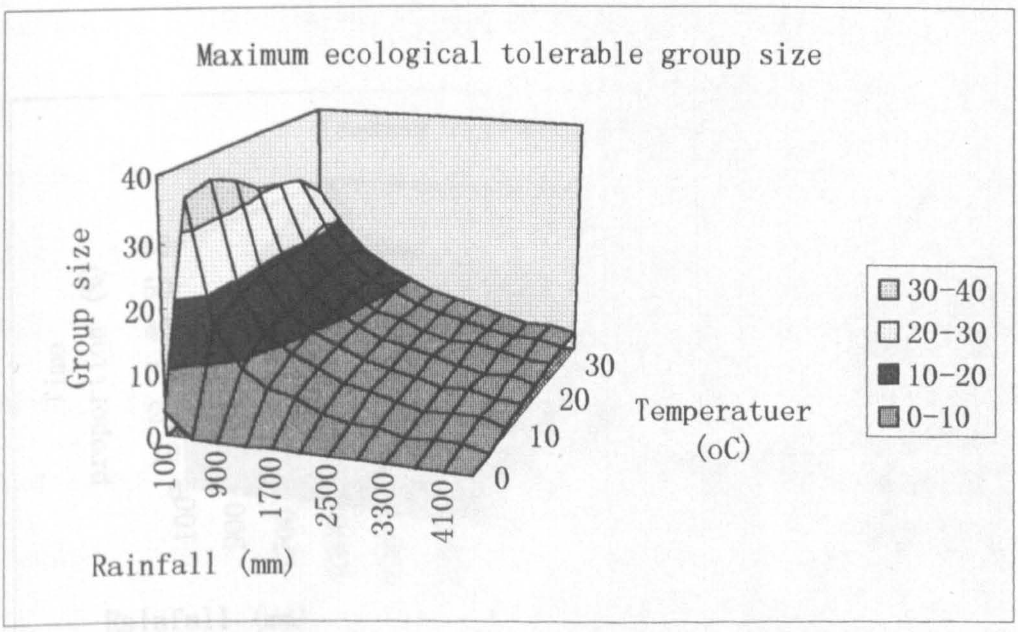


Figure 9-2. Maximum ecological group size predicted by time budget model.

Table 9-3. The feeding time proportion predicted by the model.

		Annual Temperature (℃)							
		0	5	10	15	20	25	30	35
Rainfall (mm)	100	3	27	38	45	50	54	56	60
	500	2	22	30	36	40	43	45	48
	900	2	20	29	33	37	39	41	44
	1300	2	19	26	31	35	37	39	42
	1700	2	18	25	30	33	36	37	40
	2100	1	18	25	29	32	35	36	39
	2500	1	17	24	29	32	34	35	38
	2900	1	17	24	28	31	33	35	37
	3300	1	16	23	27	30	33	34	36
	3700	1	16	23	27	30	32	33	36
	4100	1	16	22	27	30	32	33	35
	4500	1	16	22	26	29	31	32	35

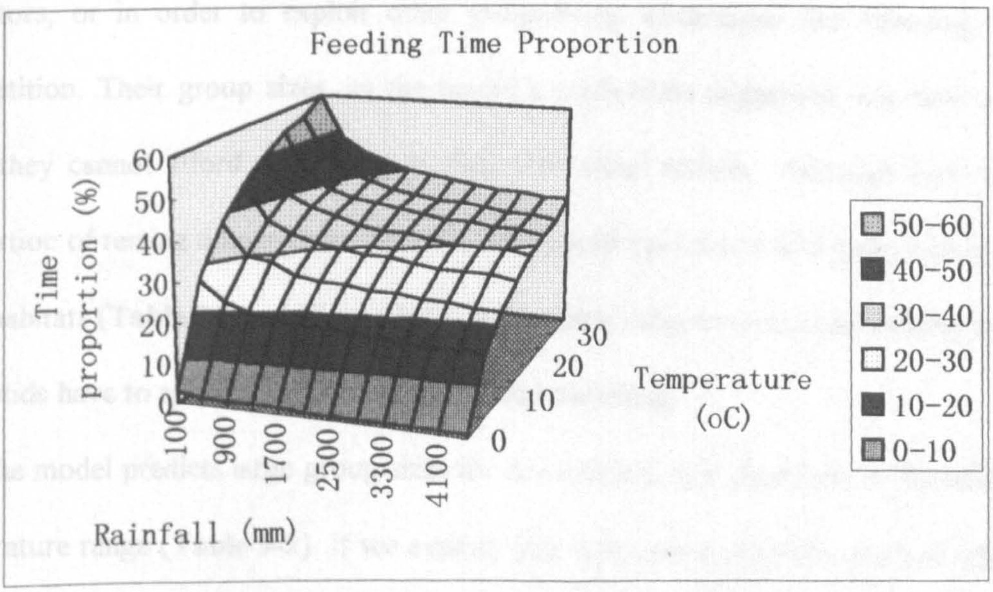


Figure 9-3. The feeding time proportion predicted by the model.

If we analyse the travelling time proportion predicted by the model (**Figure 9-4** and **Table 9-4**), we can find that they are higher than expected. Nonetheless, the general pattern seems reasonable: the lower the temperature, the higher the travelling time required and the drier the habitat, the more travelling time required. For actual gibbon habitats (between rainfall 1000-3000 mm, 10-25°C), the travelling time is between 29 and 43% and higher than feeding time. It is true that compared with other primates, the gibbons spend much more time travelling despite their smaller group size. Why should gibbons travel a lot?

Again, if we analyse the resting time as the model predicted (**Table 9-5** and **Figure 9-5**), we find that resting time is another prominent part of the gibbon's life (about 18 to 40% in typical habitats). Why cannot resting time be used as social time so as to allow gibbons to live in bigger groups? It seems that the gibbons are not forced to live in large groups to deal with predators, or in order to exploit other group-living advantages like reducing inter-group competition. Their group sizes, as the model's predictions suggested, are time constrained, since they cannot afford more time to deal with social activity. Although they have a high proportion of resting time in their daily life, their social time is low and quite evenly distributed in all habitats (**Table 9-6** and **Figure 9-6**). So the time constraint in social activity must be that hyloabtids have to spend a lot of time resting and travelling.

The model predicts large group sizes for dry habitats, and especially in the middle to high temperature range (**Table 9-2**). If we assume that most gibbon habitats are between 10 to 30 °C, and with rainfall between 1000 to 3000 mm, then the maximum ecological tolerable group size is in a range from 3 to 16, and average 8.4±3.5--- slightly bigger than the usually observed group size. These predictions are for maximum possible group size, not actual group size, so there is no requirement that gibbons have to live in groups of this size. Nonetheless, we have to ask why given that such large groups are ecologically possible, almost all gibbon species live in groups that are smaller (typically 3-6 individuals), with only a few groups reaching the maximum ecologically tolerable group size. One obvious possibility is that gibbons, unlike other species like baboons, are not just time-limited. Instead, their ecology is also constrained by other factors such as resource density or some other aspect of diet.

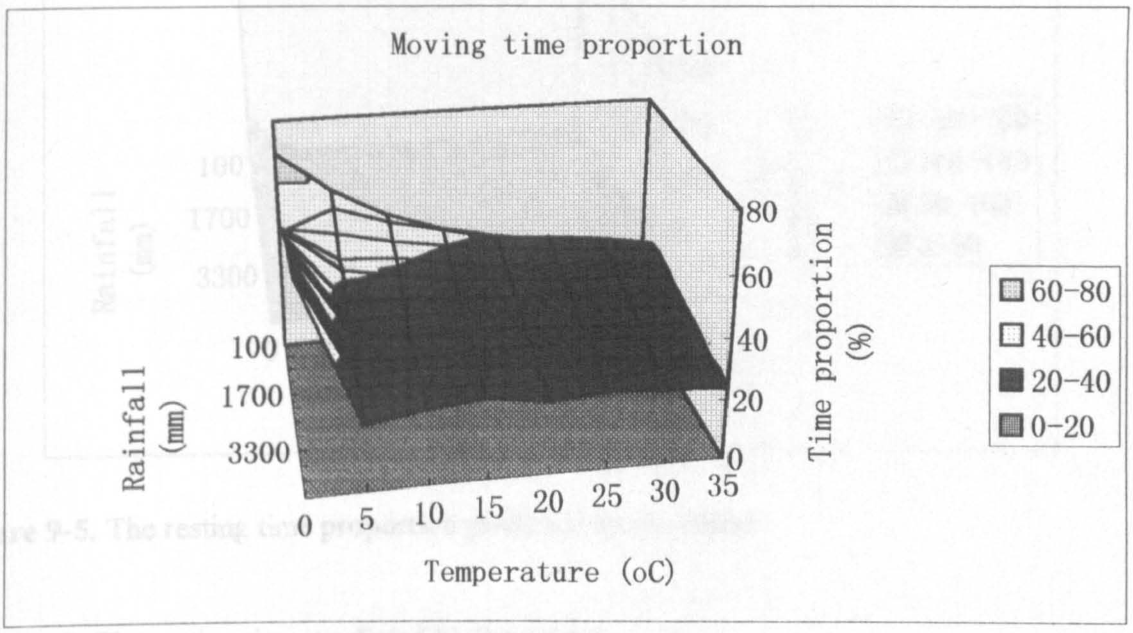


Figure 9-4. The travelling time predicted by the model.

Table 9-4. Travelling time proportion according to the model.

		Annual Temperature (℃)							
		0	5	10	15	20	25	30	35
Rainfall	100	69	55	45	39	35	32	30	27
(mm)	500	45	52	46	42	38	37	35	32
	900	50	47	43	40	38	36	35	33
	1300	54	42	41	38	36	35	34	32
	1700	57	42	39	36	35	33	33	31
	2100	59	36	35	34	33	33	31	30
	2500	61	33	34	33	32	30	30	29
	2900	63	34	31	31	31	29	29	28
	3300	65	29	28	29	29	30	28	27
	3700	66	29	29	29	27	28	26	25
	4100	67	30	29	26	27	26	27	26
	4500	69	22	25	27	24	26	25	24

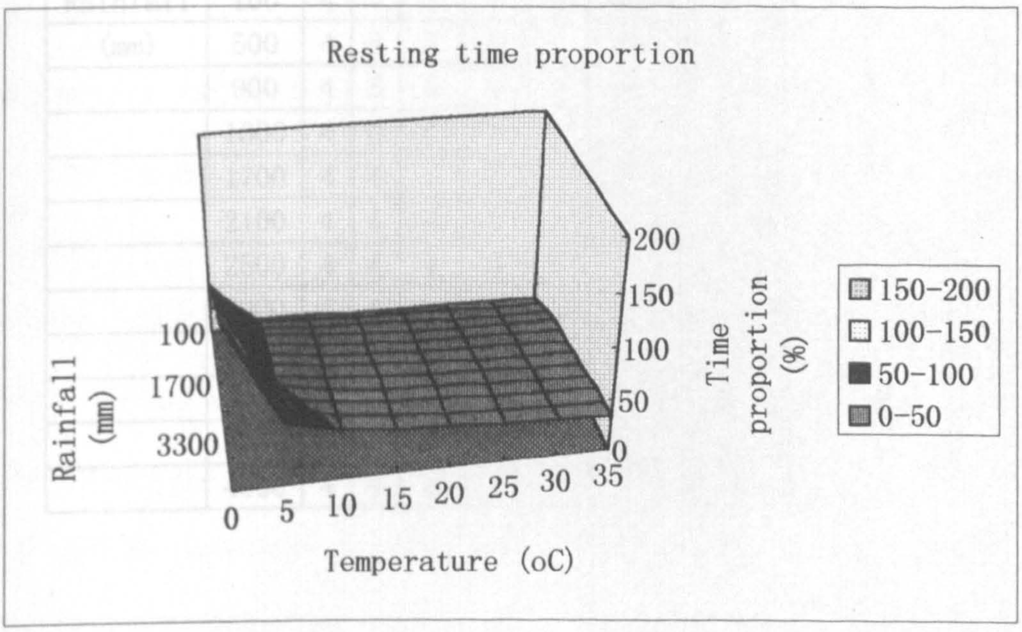


Figure 9-5. The resting time proportion predicted by the model.

Table 9-5. The resting time predicted by the model.

		Annual temperature (℃)							
		0	5	10	15	20	25	30	35
Rainfall	100	26	10	8	7	7	6	6	6
(mm)	500	56	21	17	16	15	14	13	13
	900	74	27	23	21	19	18	17	17
	1300	88	33	27	25	23	22	21	20
	1700	99	37	31	28	26	25	24	23
	2100	110	41	34	31	29	27	26	25
	2500	119	44	37	34	31	30	28	27
	2900	127	48	40	36	34	32	30	29
	3300	135	51	42	38	36	34	32	31
	3700	143	53	45	40	38	36	34	33
	4100	150	56	47	42	39	37	36	34
	4500	156	59	49	44	41	39	37	36

Table 9-6. Social time proportion predicted by the model.

		Annual Temperature (℃)							
		0	5	10	15	20	25	30	35
Rainfall (mm)	100	4	7	7	7	6	6	6	6
	500	4	5	5	6	6	6	6	6
	900	4	5	5	5	5	5	5	5
	1300	4	5	5	5	5	5	5	5
	1700	4	4	5	5	5	5	5	5
	2100	4	4	4	5	5	5	5	5
	2500	4	4	4	4	5	5	5	5
	2900	4	4	4	4	4	4	5	5
	3300	4	4	4	4	4	4	4	4
	3700	4	4	4	4	4	4	4	4
	4100	4	4	4	4	4	4	4	4
	4500	4	4	4	4	4	4	4	4

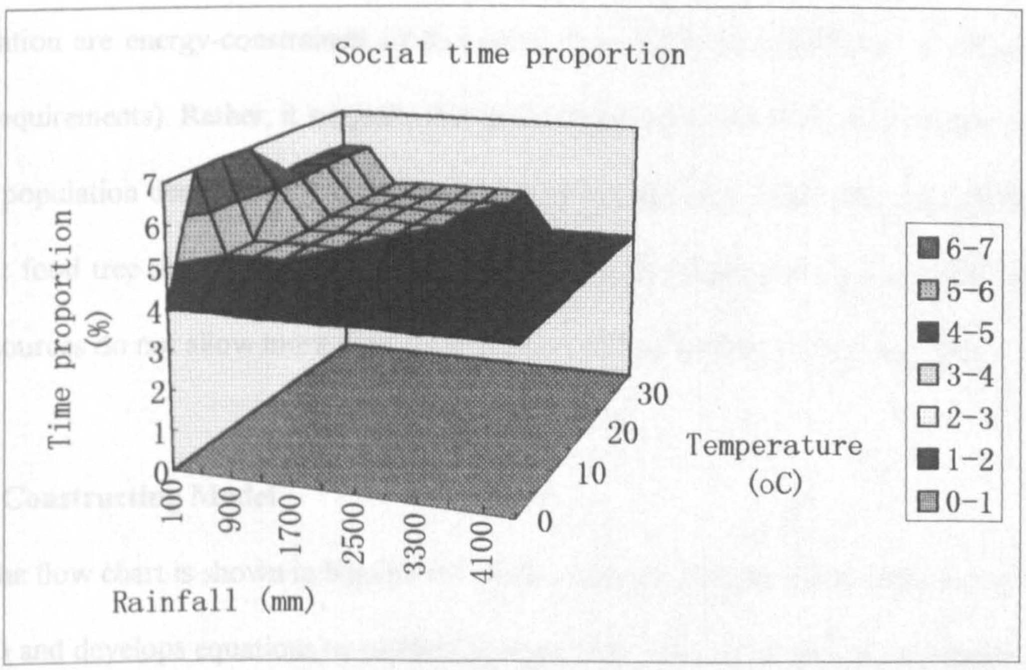


Figure 9-6. The social time predicted by the model.

9.4. Biomass Model

9.4.1. Introduction

Because the time budget model does not predict actual group size well, we may propose that the constraint of group size may not just lie in time budget but also in other aspects of their ecology. This may not be surprising because hylobatids are less social animals (*i.e.* this is in contrast to the baboon and chimpanzees) because gibbons are not forced by predation to live in large groups. Rather, group size may reflect the way that total habitat biomass has to be distributed (*i.e.* range size). So we constructed a biomass model (Model II) to predict the mean group size based on total biomass (habitat carrying capacity) and required group range size. Model II uses the relationship between population density and the variables that influence range size to predict mean group sizes from rainfall and temperature: this is to try to determine how group sizes are constrained by actual food availability. This need not imply that the population are energy-constrained (if they were, this ought to be reflected in higher feeding time requirements). Rather, it suggests that some aspect of resource distribution and patch size limits population density while at the same time requiring large range size. An example might be that food tree density is low, so requiring large areas to support a group, while individual food sources do not allow more than a few animals to feed in them of any one time.

9.4.2. Constructing Model

The flow chart is shown in **Figure 9-7**. This model starts with temperature and rainfall (as before) and develops equations to predict the size of the population and group density through intermediate variables, such as body weight, home range size. Group size is calculated by dividing the total population size (from biomass and body weight) by home range size:

POPULATION SIZE= BIOMASS / BODY WEIGHT

GROUP SIZE=POPULATION SIZE/ GROUP DENSITY.

It is already known that population size depends on biomass and body weight, and biomass can be predicted by body weight and group density. So we try to find how the environmental factors affect the home range size and body weight. We found all these variables can be directly predicted by temperature and rainfall either with a strong direct effect or through other intermediate variables, such as fig tree density and temperature variation. At first, we include all the data, including two populations with extremely large home range (*H. hoolock* and *H. concolor* respectively), but the outcomes were difficult to interpret: in typical gibbon habitats(20°C, 1700 mm), the maximum mean group size is smaller than 1 individual. When we excluded these two populations with extreme home range sizes, the model produced quite reasonable results. The equations built into the model are listed in **Table 9-7**.

Table 9-7. Regression equations for hylobatid biomass model.

Equations	R2 value	P value
TV=40.444-0.862*T	0.654	P<0.0001
Z=0.9781-0.0047*TV	0.887	P<0.0001
LAT=44.277-1.418*T	0.663	P<0.0001
LALT=19.392-3.583*LOG(T)-0.331*LOG(P)	0.680	P<0.0001
LFT=-11.173+2.082*LOG(P)-0.602*LALT	0.80	P<0.0001
LHR=-10.265+1.754*LOG(LAT)+3.328*LOG(T)+0.334*LFT	0.979	P=0.032
LGDEN=0.617+0.858*LOG(T)-0.779*LHR	0.549	P=0.008
LBW=0.917+0.084*LOG(P)-1.616*LOG(Z)-0.016*LFT	1	P<0.001
LBMS=-0.861+0.743*LGDEN+2.242*LBW	0.856	P<0.0001

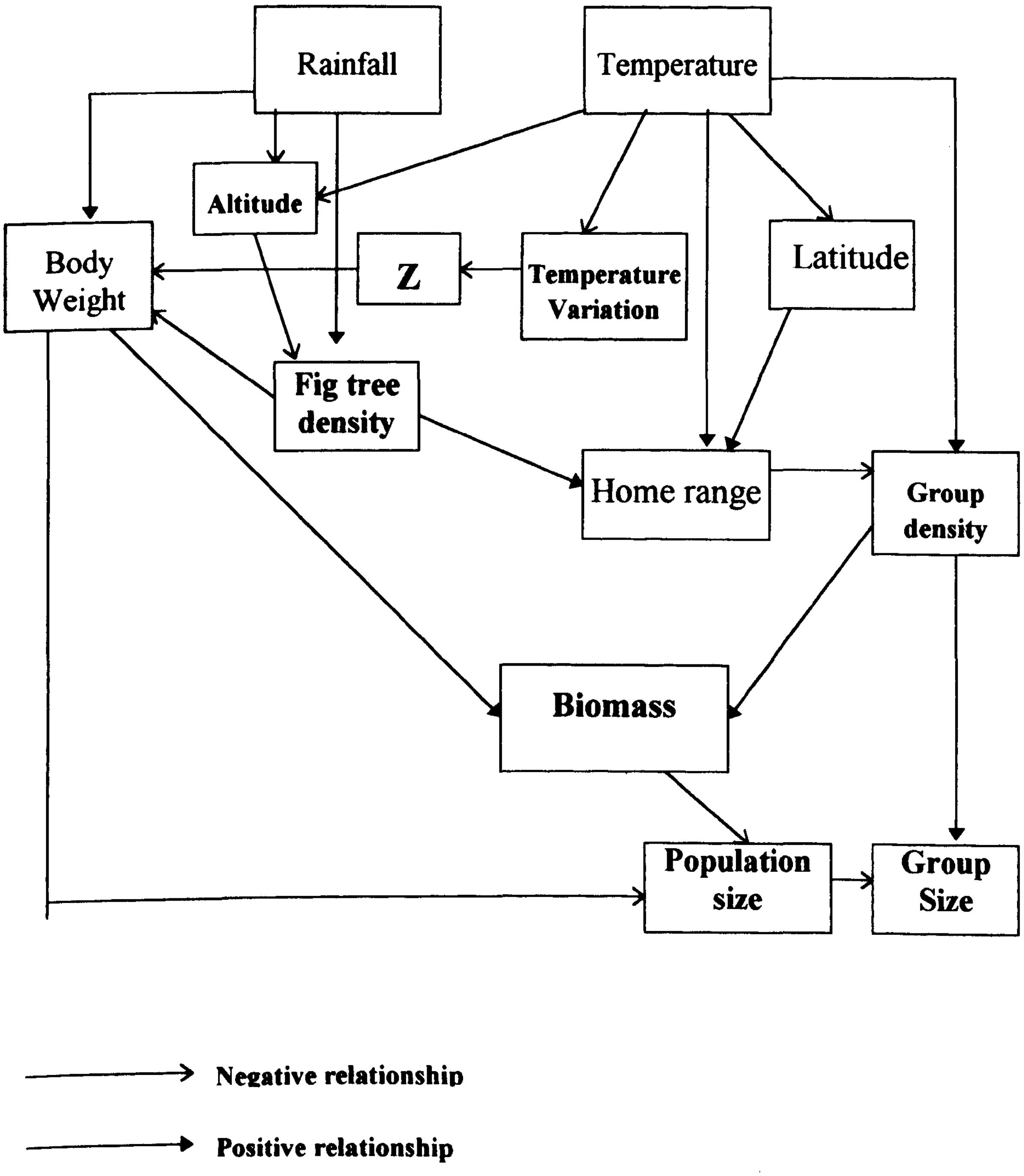


Figure 9-7. Flow diagram for the biomass model to predict the maximum resource constraint mean group size.

9.4.3. Results

As the results show (**Table 9-8**), we get a better fit to typical hylobatid mean group sizes. The predicted values fit the original cases quite well, except a few cases where lar and siamang are sympatric in habitats with high temperature (29°C) (and varied rainfall). In those sympatric habitats, predicted groups size are smaller than the predicted maximum ecologically permissible group size (**Table 9-2**) or actual group size. Some studies have suggested that the habitats where lar and siamang are sympatric are those where fig trees are abundant, and this is key to their coexistence. One explanation for this is that competition between lar and siamang artificially limits group size.

Table 9-8. The maximum group size predicted by the model based on ranging data.

		Annual Temperature (°C)							
		0	5	10	15	20	25	30	35
Rainfall	100	0. 2	1. 7	2. 2	2. 4	2. 3	2. 0	1. 2	0. 4
(mm)	500	0. 3	2. 4	3. 1	3. 3	3. 3	2. 9	1. 7	0. 6
	900	0. 3	2. 7	3. 5	3. 8	3. 7	3. 2	1. 9	0. 7
	1300	0. 3	2. 9	3. 8	4. 1	4. 0	3. 5	2. 1	0. 8
	1700	0. 4	3. 1	4. 0	4. 3	4. 2	3. 7	2. 2	0. 8
	2100	0. 4	3. 2	4. 2	4. 5	4. 4	3. 9	2. 3	0. 9
	2500	0. 4	3. 3	4. 3	4. 7	4. 6	4. 0	2. 4	0. 9
	2900	0. 4	3. 5	4. 5	4. 8	4. 8	4. 2	2. 5	0. 9
	3300	0. 4	3. 6	4. 6	5. 0	4. 9	4. 3	2. 5	1. 0
	3700	0. 4	3. 6	4. 7	5. 1	5. 0	4. 4	2. 6	1. 0
	4100	0. 4	3. 7	4. 8	5. 2	5. 1	4. 5	2. 7	1. 0
	4500	0. 5	3. 8	4. 9	5. 3	5. 2	4. 6	2. 7	1. 0

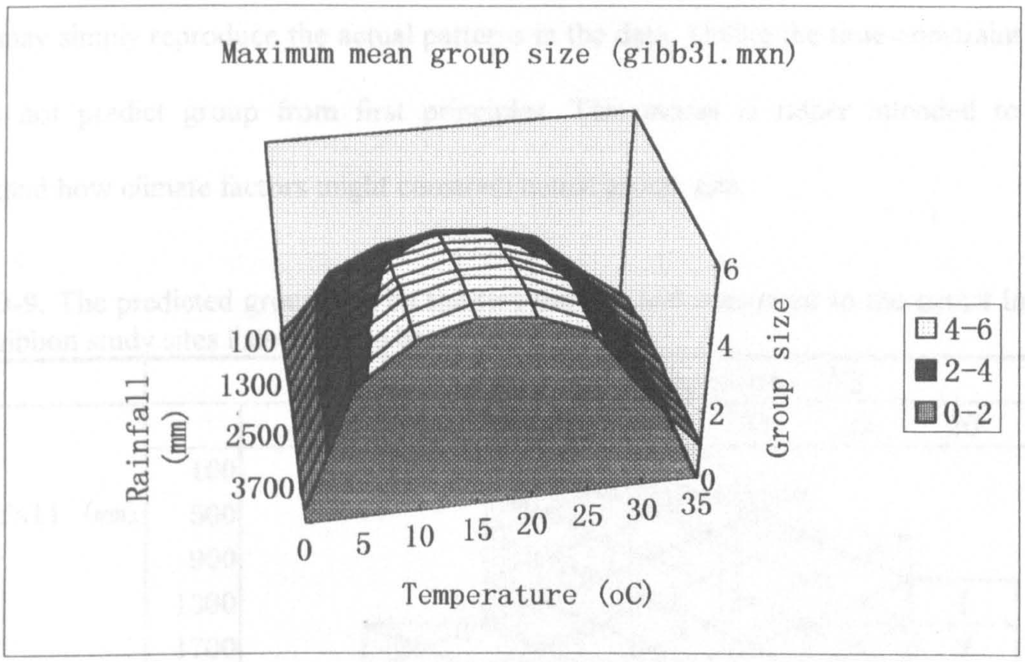


Figure 9-8. Maximum mean group size predicted by biomass model.

Both **Table 9-8 and Figure 9-8** show that group size was highest when rainfall is highest, in the middle ranges of temperature (about 15 to 20°C). To either side of this temperature zone, group size declines. Although hylobatids could in theory live in habitats where temperatures are at or below freezing or hotter than 35 °C (as Model I predicts), maximum mean group sizes are small in these habitats: in area of 4500 mm rainfall, the maximum group size is 1 individual or less.

We can see the gibbons prefer habitats with high rainfall and moderate temperatures. Rainfall might be not the direct factor which determines habitat quality, as discussed above, but rainfall reflects the humidity or water supply for vegetation growth and maintenance.

It is worth noting that the model predicts similar or even larger group size in the cool high altitude/high latitude habitats of Yunnan. If this is true, then it would explain why polygyny is more frequent in these habitats. This could imply that, contrary to earlier beliefs, these habitats are relatively not bad quality for gibbons---- that is why they can live there or even maintain large groups. It should be noted that biomass model is based on actual group sizes, and so the model may simply reproduce the actual patterns in the data. Unlike the time-constraint model, it does not predict group from first principles. This model is rather intended to try to understand how climate factors might constrain actual group size.

Table 9-9. The predicted group size by the two models and compared to the actual locations of the gibbon study sites listed in data base*.

		Annual Temperature (℃)							
		0	5	10	15	20	25	30	35
Rainfall (mm)	100								
	500			☒	☒	☒ 1			
	900			☒	☒	☒	☒		
	1300			☒	☒	☒	☒	1	
	1700		☒	☒	☒	☒ 2	☒ 1	2	
	2100			☒ 1	☒ 2	☒	☒	2	
	2500			☒	☒	☒ 1	☒ 1		
	2900				☒	☒	☒		
	3300					☒	☒ 5		
	3700						☒		
	4100						1		
	4500								

* Number in plots are populations studied located in the plot according to data set.

9.5. Gibbon Distribution Pattern Based on the Two Models

Table 9-9 combines the results of the two models in order to determine where gibbons can survive. This is done by highlighting those cells where the predicted mean group size in **Table 9-8** is greater than 3 but smaller than N_{max} (not smaller than 4, as given in **Table 9-2**). We can then ask whether the model predicts the actual gibbon distribution at all by using a goodness-of-fit test (X^2 test). Fourteen gibbon study sites occur within the area defined as capable of supporting gibbons, and only 6 fall outside it. If these sites were distributed at random, within the habitats contained in **Table 9-9**, we would expect only 30/96 of them to do so. The observed distribution differs significantly from that expected if gibbon populations were unconstrained (**Table 9-10**: X^2=13.486, df=1, p<0.001).This means that the models give a good fit to the actual distribution patterns.

Table 9-10. The contingency table showing the number of cells where gibbons presence/absence of gibbon populations in relation to the predictions from the model.

	Occur	Cannot occur	Total
Predicted by model	30	66	96
Expected	6.25	13.75	20
Observed	14	6	20

X^2=13.468, df=1, P<0.001.

9.6. Discussion and Summary

In this chapter a time constraint model and a biomass constraint model are presented. The first model predicts a low maximum ecological tolerable group size, and the second model predicts actual mean group size that are usually smaller than that maximum ecological tolerable group sizes which are mainly determined by the social time available. These results suggest that hylobatid group size is time-constrained. According to the model, the gibbons could live in much large groups in most typical habitats, especially with low rainfall and high temperature, but cannot live in those habitats with temperatures around freezing and very high rainfall. Actual mean groups sizes, which are usually smaller than the maximum ecological tolerable group sizes in typical habitats, are mainly determined by food availability. The predictions of the biomass model are quite accurate, suggesting that the actual gibbon group sizes are mainly energy-constrained. Gibbons thus differ from the other taxa for which models have been developed (baboons, chimpanzees) in that all these other species are mainly time-constrained. In contrast to the time budget model's prediction, the biomass model predicted that high rainfall does not seem to limit group size, but gibbons cannot live in habitats annual temperatures are higher than 30°C, or in habitats with low rainfall (about or less than 300 mm). High rainfall might imply good habitat quality, when it is warm enough.

Based on the data set and the models' predictions, it seems that the present black gibbon habitats in China are not marginal habitats, even though they live in much colder and drier areas than tropical area of other hylobatids. The time constraints model suggested that it would be possible for gibbons to live much further north if it is dry enough (it is dry in northern China), but the habitat in northern China cannot support a high enough density of animals, and this ultimately limits the taxon's distribution. As we know, the macaques (*Macaca*) can live much further north near the latitude 40° line (Quan, *et al.*, 1981a, b; Zhang *et al*, 1981), and usually in bigger groups, so it should be possible for gibbons to live there if we consider only their time budgets. However, the habitat there cannot support a high enough carrying capacity allow gibbons to survive.

The time budget model suggests that in their typical habitat (with its low temperature ca. 10°C, 1000-2500 mm rainfall), black gibbons can live in a relatively large groups (4-9), that are sufficient to allow a mixture of polygyny and monogamy. That size is larger than those typical of other gibbon group size (2-6). We can propose that, black gibbons can either adopt polygyny or monogamy as their mating strategy, and when sex ratios are skewed, due to hunting, habitat fragmentation or skewed reproduction in small populations, some are able to form polygynous groups. The actual group sizes predicted by the biomass model do not support the possibility of habitual polygyny in black gibbons or in other hylobatids.

CHAPTER 10. CONCLUSION

10.1. New Findings from This Study

When reporting the polygyny of black gibbons in Yunnan, a northerly and high altitude hylobatid species, Haimoff *et al.* (1987a) proposed that their habitat underwent a shortage of fruits in some seasons. Since their work, more data about this unique species have become available, although not systematically sampled (Chen, 1995; Haimoff *et al.*, 1986; 1987a; Jiang *et al.*, 1994a, b, c; 1999; Jiang and Wang, 1997; Lan, 1989, 1993; Sheeran, 1993, 1995). Except for climatic data for one site (Xujiaba, Chen, 1995), seasonal variation in time budget, feeding proportion, day journey length and home range size are not well understood; neither are food availability and its seasonal variation. The available data are variable in quality, possibly owing to the methodology used. The better studies to date (Lan, 1989, 1993; Chen, 1995) are on middle-size groups, and our understanding of the ecology and behaviour of large groups is limited (Liu *et al.*, 1989). Although data in these publications provide some good basic knowledge, more effort is required to fill in the gap of our knowledge of hylobatids (as the black gibbons represent an extreme habitat strategist) and for effective conservation. In order to understand the selection forces shaping polygyny among hylobatids (especially in black gibbons), I undertook a comparative study on black gibbon behavioural ecology between two habitats [one primary forest habitat (Chen, 1995) and one habitat with lots of human disturbance, like cutting, burning and grazing]; and continued to observe a group changing from pair-living to two-female group.

Until now, some multi-female groups of black gibbons have been reported to occur at Xiaobahe and its adjacent area (habitat with more human disturbance), but only very rarely (if at all) at Xujiaba (a habitat with less human disturbance). Both group density and biomass are higher at Xiaobahe than that at Xujiaba (Lan, 1995a). The differences in habitat quality between the two sites are possibly the best explanation for these differences and evidence to support a resource polygyny threshold model in this species. The present study reveals that food availability is much richer at Xiaobahe (*vs.* Xujiaba): both tree diversity and liana diversity are higher, especially liana diversity; and fig trees are available at Xiaobahe, but not at Xujiaba. Comparison of the habitat between other sites, such as Xiaobahe-Kainanhe, and the habitats occupied by black gibbons in Central Yunnan and hoolock gibbons in west Yunnan seem to support a resource polygyny threshold model, too.

However, detailed habitat comparison for two kinds of groups (*i.e.* one-female group *vs.* multi-female group), either within Xiaobahe or at other sites, suggest that habitat difference between single-female and two-female groups are not marked: two-female groups do not always live in richer habitats. In the case of group B, which I have monitored changing from pair-living to two-female groups, its habitat did not seem to improve too much as it changed group structure. This could be interpreted as suggesting that groups become multi-female group when external factors (habitat destruction by human) prevent maturing animals from emigrating. So at present, we should be careful not to conclude that the resource polygyny threshold model applies well in black gibbons. If possible, some well-planned studies with good experiments, like calling playing-back, DNA-fingerprinting analysis through faeces, etc., will be very helpful in understanding the 'polygynous' in this gibbon species.

10.2.The Differences Between Gibbon Species

It seems that the black gibbons are ecologically similar to other hylobatids. When comparing black gibbon with other gibbons and siamang, very few differences were found. It seems that intra-species differences are more marked than the inter-species differences. Their time budgets are not unique among gibbons, although they have a relatively low proportion of feeding time and higher resting time. There is variation between seasons, with resting being more common in the wet season with a possibly longer active period. Their diet is also within the general range of all gibbons, but with a high proportion of leaves similar to siamang. But the black gibbons consume a lot of fruits when ripe fruits are available. Seasonal (or monthly) variations in diet are clear: the black gibbons' diet changed from frugivory to folivory and back again. This variation is not only limited from month to month, but also from day to day. Black gibbons used the habitat in similar ways to other gibbon species, with uneven use concentrated in some parts of their home range. Their major difference might lie in the larger home range size, and with little territorial behaviour, in black gibbons.

Much differences in ecology are between gibbons and siamang, and this difference can be explained by the heavier siamang body weight and the competition between siamang and smaller gibbons since siamang are always sympatric with smaller gibbons. The difference between black gibbons and other allopatric gibbons may reflect the poor habitat of black gibbons. The most northerly black and hoolock gibbons differ from the other gibbon species in with a greater degree of folivory, presented in some populations or varied from season to season in the same population.

10.3. Lessons From the Social Systems Models

I have presented two models, one a time constraint model (time budget model), the other a resource constraint model (biomass model). The time budget model predicts a low maximum ecological tolerable group size, but the biomass model predicts actual mean group size that are usually smaller than that.

Maximum ecological tolerable group sizes as the time budget model predicted are mainly determined by the social time available. According to the model, the gibbons could only live in much large group in habitats with low rainfall and high temperature, but cannot live in those habitats with low temperatures around freezing and very high rainfall.

Actual mean group sizes, which are usually smaller than the maximum ecological tolerable group sizes in habitats, are mainly determined by food availability. The predictions are quite accurate, suggesting that the actual gibbon group sizes are mainly resource-constrained. Gibbons thus differ from the other taxa for which models have been developed (baboons, chimpanzees) in that all these other species are mainly time-constrained. The biomass model suggests that gibbons cannot live in habitats where annual temperature is near freezing or where temperatures are higher than 30°C, or in habitats with low rainfall (less than 300 mm). In contrast to the time budget model predictions, high rainfall does not seem to limit group size according to the biomass model. The high rainfall might imply good habitat quality, when it is warm enough.

Based on the data set and the model's predictions, it seems that the present black gibbon habitats in China are not marginal habitats: they could live in much colder and drier areas. As we know, the macaques (*Macaca*) can live much further north near latitude 40° (Quan *et al.*, 1981a, b; Zhang *et al.*, 1981) and usually in bigger social groups. The time constraints model suggested that it would be possible for gibbons to live there too if it is dry enough (and it is dry in northern China), but the biomass model suggests that the habitat there cannot support a high enough density of animals, and this ultimately limits the taxon's distribution. The reason for poor habitat quality there is owning to the low temperature (or high temperature variation) and low rainfall (or uneven rainfall distribution) there.

10.4. Are Black Gibbons Folivorous?

Although black gibbons consume a high proportion of leaves in their diet, we cannot confidently declare that the black gibbon is absolutely folivorous, rather than a flexible opportunistic feeder. Their favourite foods are fruits, and they consume a lot when available. Both fruits and leaves in the diet are varied from time to time in the groups we studied. If their high folivorous diet is evolutionarily adaptive (like that of langurs), then we should expect few or no differences in the proportion of leaves in the diet between less disturbed and highly disturbed habitats; or between different months for the same habitat. When fruit are available and abundant, fruit are their main food source and leaves are fed on less intensively although usually not totally avoided.

10.5. Are Black Gibbons Polygynous?

Field surveys and studies suggest that the black gibbons are not wholly always polygynous as in many other primates, but a mixture of mainly monogamy and polygyny. As our results suggested, if there are multi-female groups, they are usually two-female groups--- with two adult females. What do the models' predictions tell us about this puzzling question?

The time budget social systems model suggests that in their typical habitat (with low temperature ca. 10°C, 1000-2500 mm rainfall), black gibbons can live in relatively large groups (4-9), sufficient to allow a mixture of pair-living and multi-female grouping. That size is larger than those actual group size in other gibbons species (2-6). We can propose that, in black gibbon's habitats without resource constraints, gibbons can either adopt polygyny or adopt monogamy as their mating strategy. When sex ratios are skewed, due to either habitat fragmentation or skewed reproduction in small populations, some gibbons form multi-female groups (typically with two females). But this model predictions also suggest that the other gibbons can allow two kind of groupings in their typical habitat.

However, the actual group size predicted by the biomass social systems model do not support the possibility of multi-female grouping as a regular features of black gibbons or other hylobatids. This model suggests that group sizes of black gibbons are similar to other gibbons although the time budget model suggests other gibbons can have bigger group size. In conclusion, both models do not suggest that multi-female grouping or polygyny would be regular features in black gibbons.

Although monogamy is still presumed to be the basic mating system in hylobatids, flexibility is possible. Some recent studies have argued that monogyamy is not rigid, and grouping flexibility has been a topic of some considerable interest in the past decade (Ashan, 1994; Brockelman *et al.*, 1998; Jiang *et al.*, 1999; Palombit, 1994,1995, 1996; Reichard, 1995). Social systems are generally genetically determined, but they are not just genetically determined because the habitat itself is important in shaping social systems (habitat-constraint), specifically in disturbed habitats (Jiang *et al.*, 1994b).

10.6. Why are Black Gibbons Polygynous?

It is possible that habitat disturbance prevents group members dispersing, and this gives rise to multi-female grouping and polygyny. If this is the case, evidence suggesting tolerance between adult females (mother- daughter) and the availability of enough food to support larger groups are needed. Our study groups adapt to the disturbed habitat well, adult females within the groups do not conflict with each other and showed successive successful reproduction. This suggests that the adult females can tolerate each other and that food availability was enough within the home range. The black gibbons can be very flexible in their feeding strategies, and this might imply no resources constraint when the group size is not very large (e.g. less than 10) as discussed above.

In most sites with multi-female gibbon groups, it seems that the habitat has suffered quite serious disturbance from human beings. In Hainan, the small black gibbon population (about 20 individuals or less) is limited to a patch of forest about 12 km^2, logging and hunting was not uncommon in the past. Even after the nature reserve has been established, some forest patches suitable to and inhabited by gibbons were later destroyed by logging (Zhang *et al.*, 1995). The situation in Yunnan is similar (Lan, 1995b): all nature reserves with gibbons in Yunnan are easily accessed for logging, hunting and other activities. Some activities, such as cutting down a big tree just for little wild honey or some fruits, bring deterioration to the forest. Some of the trees cut down for this purpose are more than 80 cm in dbh, and possibly more than 1000 years old. Other activities, such as hunting, directly effect the gibbon populations.

The field research has showed that black gibbons are possibly territorial but only very weakly. The group calls a lot in the morning and this is assumed to be territorial advertisement. Only one conflict has, however, been recorded (Sheeran, 1993). If the black gibbon is polygynous, there are three possibilities as to the cause: 1) no other breeding options are available to females in the population; 2) the females actively choose polygyny on a good territory rather than monogamy on a poor one; or 3) females are deceived into polygyny. Since the two females are observed in the same cohesive group, and they act together, the third possibility is unlikely.

Then how about the other two explanations? The second explanation would require there to be unmated males on peripheral territories, but none have in fact been observed. We have heard some solitary male solo calls, usually along the breeding group's territory border, and one possible solitary male was observed (Lan *et al.*, 1990). Both the lone male observed (Lan *et al*, 1990) and heard (Lan, 1990, unpublished data) at Xujiaba, were in good quality habitat without habitat fragmentation; yet no multi-female groups were observed (Lan *et al.*, 1989, Chen, 1995) (**Chapter 3**). At Xiaobahe, a solitary male's solo was heard in 1997-8, but it was close to the territory of group C3 or G, where the habitat in general is continuous. At this place, Jiang *et al.* (1994a, b, 1999) reported that polygynous groups occurred. In general, all these analyses suggest that the second explanation is not the best choice. This leads us to favour the first hypothesis, that polygyny occurs where gibbon group have no alternative breeding options available. The lack of breeding opportunities could be due to habitat fragmentation.

10.7. Feeding and Social Grouping Patterns

The habitat quality variation in black gibbons' ranges might have influence on its grouping patterns as it is in the spider monkeys. Robbins *et al* (1991) suggested that the size and density of food and its distribution patterns might correlate with the different social grouping patterns in spider monkeys and gibbons. These two kinds of primates are similar in diet, body size, and locomotion patterns, but differ in grouping patterns. Gibbons live in small stable groups, but spider monkeys form unstable groups which change size in different seasons. They tested three predictions with some success about food size and density and its variation, and they concluded that there was not sufficient variability in food availability in gibbon's habitat, and hence concluded that the low level of food abundance for gibbons might account for the gibbon's stable small groups in contrast to the fission-fusion system of the spider monkeys. If this is the case, then the variable habitat of black gibbons may be similar to the spider monkey's habitat, and this might explain why black gibbons have larger group sizes and sometimes undergo fission-fusion-like patterns (Liu et al, 1984; Jiang et al., 1994a).

Black gibbons live in the most northerly latitudes and highest altitudes of all gibbons, and suffer from different ecological constraints, including varied food size and density. These environmental factors could contribute to the variation in social patterns in this species.

10.8. Implications for Conservation

Conservation is always a concern in primate field study, for most primates are undergoing a risk of extinction. The black gibbons is facing a similar fate. One subspecies, *Hylobates concolor hainanus*, was reported to have only 15 individuals left in a nature reserve a few years ago (Wang, 1995), and its current situation is not known at all. For conservationist, it is important to know what kind of measures can be taken to let the available populations healthy.

Human's interference are the major source threaten gibbons' survival. The most important long-term threat to their survival, and also the most difficult to counter, are habitat destruction, degradation and fragmentation. While gibbon populations may recover from past hunting, habitat destruction can put a ceiling on the size of the total population and restrict its range. It might take longer time to reforest an area naturally to finally suitable for the living of gibbons. Black gibbons in China have suffered severely from past habitat destruction, with the result that all populations are now restricted to small remnants of natural forest, all but two of which are well under 50000 ha in size (Bleisch and Chen, 1990; Haimoff *et al.*, 1986; Lan, 1995; Liu *et al.*, 1987; Yang *et al.*, 1987; Zhang *et al.*, 1995).

Even if hunting, habitat destruction and habitat degradation are all controlled, remaining gibbon populations may still not be secure. Even in some well-protected nature reserves, such as Mts. Wuliang and Mts. Ailao, fragmentation of gibbon population by past habitat destruction has created an unseen threat that may go undetected. Most populations of gibbons in China are quite small and few if any are above a threshold of 50 adult individuals. This in itself should be cause for concern, but even if the total population of gibbons in a protected area is large enough to give confidence in its viability, the population may actually be fragmented into many small, isolated habitat "islands". This may affect the long-term viability of populations in a number of ways (see Soule, 1987 and Caughley and Gunn, 1996 for overviews). One impact of fragmentation on gibbons may be to limit the availability of suitable mates for unmated gibbons, an effect that is especially severe in primates that live in small family groups.

In China, fragmentation of black gibbons into small sub-populations has been documented in the Mts. Wuliang and Mts. Ailao (Bleishc and Chen, 1990, Lan, 1995, Zhang *et al.*, 1995) and many gibbon populations may already be threatened from the effects of small population size or habitat fragmentation. It is necessary to counter these threats with programs for habitat rehabilitation to reconnect isolated sub-populations. Stopping habitat destruction and degradation should be emphasised first in taking any conservation action, such as burning and cutting.

The black gibbons can live in cool, although not very cold habitat. Our study suggested that the present Chinese habitat are not the marginal habitat, but it might be not the best for them. Undoubtedly, the negative interference from human on the habitat should be prohibited. However, for positive conservation purpose, human interference on the habitat is necessary, but it should be very careful since it is difficult to control and it is difficult to know how much is suitable. Too much interference might destroy some vital conditions which may lead to the extirpation. So in general, it is better not to introduce human interference before we know more about the real natural process of the gibbon population and the human actions can really be controlled. Some change is so trivial, and it can be hidden for so long time, that we do not really know what will happen to them in the future. However, some limited human activities like planting food species around corridor forest might be helpful to improve the habitat quality and promote the gibbons' survival probability.

We know that the home range of black gibbons are usually large. Isolation of the forest patches is not so serious if there are some shrubs available between good forest patches, as the present study group showed, so it is important to protect all even if the habitat looks as bad as waste land. To nature, waste land is not really waste land. So those areas which really need to be improved to keep the gibbons connection, require very careful management. Available trees and shrubs should never be destroyed, and some new seedlings should be planted to promote the cover of trees. For all habitats, either primary or secondary, we should not cut trees or shrubs which we think are of no use to gibbons, but improve the composition by adding some other useful trees or liana species. As forest *Alnus nepalensis*, which is a very common forest type on disturbed land in Yunnan, they might be restored sooner to be suitable to gibbons. Some diet species, like *Myrica esculata*, *Prunus* sp. and *Betula luminefera*, are recommended as our study showing their value to gibbons. These species adapt to the opened area well, and naturally developed after primary forest degradation. These trees can provide both roosts and foods for gibbon groups.

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APPENDIX I. PLANT SPECIES AND PARTS EATEN BY BLACK GIBBONS

NOTES:

Food parts: **L**-leaves, include mature leaves, young leaves, leaf buds and shoots(**Sh**); **Fl**-flowers, include flower buds; **Fr**-fruits, include seeds (**Sd**) and fruit pulps.{As classified by Y.Z. Zhang et al (1995), the fruits included fruits, berries, nuts, seeds, drupes, capsules, nutmegs, all of them are included in **Fr** (fruits) in the table below.}

Authors: **LD1**-Lan (1989a, 1993); **SL2**-Sheeran(1993: 167); **CN3**-Chen(1995: 91-92); **ZQ4**-Zhang et al.(1995:207-208); **YX6**-Yang and Xu (1990), **LD5**-present study. The final one study was not carried at Mt. Wuliang and Mts. Ailao, but at Mts. Bangma in Gengma County. The others abbreviations are **HY**-Haimoff et al.(1987); **BC**-Bleisch and Chen (1991) --- in the column of **CN3**.

- with phenological records at Xiaobahe and Xujiaba

Family	Species Name	Chinese name (Local Name)	Parts eat: L Fl Fr Sh Sd Ly	LD 1*	SL 2*	CN 3*	ZQ 4*	LD 5*	YX 6*
Magnoliaceae	*Manglietia insignis*	红花木莲#	Fl/L			+		+	
Magnoliaceae	*Michelia floribundex*	多花含笑#	Fl/L			+		+	
Illiciaceae	*Illicium macranthum*	大花八角#	Fl?			+			
Schisandraceae	*Kadsura ciccinea*	冷饭团#	Fr/L/Fl						
Schisandraceae	*Schisandra chinensis*	吊吊香		+	+	HY			
Schisandraceae	*Schisandra* sp.	五味子藤	Fr						
Lauraceae	*Cinnamomum tamala*	柴桂#	Fr? Sh						
Lauraceae	*Machilus bombycina*	绿毛桢楠#	L?		+				
Lauraceae	*Machilus viridis*	绿叶润楠# 黄心树	L			+			
Lauraceae	*Litsea cubeba*	山苍子# （山胡椒）	Fr/L/Fl					+	

Family	Species Name	Chinese name (Local Name)	Parts eat: L Fl Fr Sh Sd Ly	LD 1*	SL 2*	CN 3*	ZQ 4*	LD 5*	YX 6*
Lauraceae	*Lidera thomsonii*	汤氏山胡椒	Fr/Ll					+	
Lauraceae	*L. elongata*	黄丹木姜子	L/Fl			+		+	
Lauracear	*Neolitsea polycarpa*	多果新木姜	Fr			+			
Ericaceae	*R. irroratum*	露珠杜鹃#				+			
Ericaceae	*Rhododendron delavayi*	马缨花#	Fl	+				+	
Ericaceae	*Rhododendron leptothrium*	薄叶杜鹃#	L			+			
Ericaceae	*Lyonia ovalifolia*	珍珠花# (南烛)	L, L(变态叶 芽)			+		+	
Actinidiaceae	*Actinidia callosa*	猕猴桃#	Fr/Fl/L					+	
Actinidiaceae	*A. glaucocallosa*	猕猴桃#	Fr/Fl/L			+		+	
Betulaceae	*Betula alnoides*	西南桦	L			+			
Betulaceae	*B. luminifera*	亮叶桦#	L/叶芽					+	
Betulaceae	*Alnus nepalensis*	旱冬瓜#	芽?			BC			
Elaeagnaceae	*Elaeagnus conferta*	密花胡秃子#	Fr	+		+	+		
Elaeagnaceae	*Elaeagnus sp.*		Fr	+					
Saurauiaceae	*Saurauia napaulensis*	水冬哥	Fr				+		
Myrtaceae	*Syzigium angustini*	普桃	Fr				+		
Elaeocarpaceae	*Elaeocarpus japonicus*	薯豆（山桃）#	Fr		+			+	
Elaeocarpaceae	*E. braceanus*	（山桃）#	Fr		+			+	
Elaeocarpaceae	*E. howii*	（山桃）#			+			+	

Family	Species Name	Chinese name (Local Name)	Parts eat: L Fl Fr Sh Sd Ly	LD 1*	SL 2*	CN 3*	ZQ 4*	LD 5*	YX 6*
Elaeocarpaceae	*Elaeocarpus* spp.	（山桃）#		+				+	
Rosaceae	*Eriobotrya bengalensis*	南亚枇杷#						+	
Rosaceae	*Docynia delavayi*	多依							
Rosaceae	*Eriobotrya serrata*	（枇杷）			+				
Rosaceae	*Prunus undulata*	云南欧李#	Fr	+				+	
Rosaceae	*Prunus* sp.	(樱桃)		+				+	
Rosaceae	*Prunus conradinae*		Fr.				+	+	
Rosaceae	*Cerasus cerasiodes*	冬樱花	Fr/L					+	
Rosaceae	*Prunus maximowiczii* var. *Adenophora*	具腺马氏樱（白樱花)#	Fr/L	+				+	
Rosaceae	*Sorbus ochracea*	黑毛花楸#	Fr					+	
Rosaceae	*Crataegus scabrifolia*	山茶	Fr				+		
Rosaceae	*Stranvaesia davidiana*		Fr				+		
Rosaceae	*Cotoneaster buxifolius*	黄杨叶荀子	Fr				+		
Rosaceae	*Rosa longicuspsis*	常绿蔷薇#	?				+		
Rosaceae	*Rubus dielsianus*	迪氏悬钩子#	?						
Rosaceae	*Pyrus pashia*		Fr				+		
Rosaceae	*Stranvaesis davidianna*	红果树	Fr				+		
Rosaceae	*Rubus niveus*	红泡刺藤							+
Rosaceae	*Rubus Ichangensis*	黄泡子							
Rosaceae		大果花楸							
Celastraceae	*Celastrus* spp.	南蛇藤#	Fr					+	
Moraceae	*Ficus sarmentosa*				+				
Moraceae	*Ficus* spp.	榕	Fr/Sh	+					
	Ficus virens	黄葛树#	F					+	
Campanulaceae	*Gynostemma pentaphyllum*	绞股兰	Ly/Sh	+					

Family	Species Name	Chinese name (Local Name)	Parts eat: L Fl Fr Sh Sd Ly	LD 1*	SL 2*	CN 3*	ZQ 4*	LD 5*	YX 6*
Rutaceae	*Zanthorylum alpinum*	高山花椒	?						
Rutaceae	*Toddalia asiatica*	飞龙掌血#	Fr					+	
Rutaceae		茵芋							
Lardizabalaceae	*Holboelia fargesii*	五叶瓜#		+		+		+	
Lardizabalaceae	*H. oratifoliolata*				+				
Lardizabalaceae	*H. deaibatus*				+				
Lardizabalaceae	*H. latifolia*	五风藤	Fr/L/Fl						
Lardizabalaceae	*Holboelia*				+				
Lardizabalaceae?	*Decaisnea insignis*	猫儿屎	Fr				+		
Lardizabalaceae?	*Decaisnea fargesii*		Fr				+		
Vacciniaceae	*Vaccinium duclouxii*	米饭树#	Fr						
Vacciniaceae	*V. mandarinorum*	米饭树	Fr?/L/Fl			+			
Sabiaceae	*Sabia*	清风藤		+					
Meliosmaceae	*Meliosma cuneifolia*								
Meliosmaceae	*M. kirkii*	山青木#	L			+		+	
Viscaceae	*Viscum articulatum*	寄生（螃蟹脚）#	Fr				+	+	
Loranthaceae	*Taxillus* sp.	寄生#		+				+	
Araliaceae		罗伞							
Araliaceae	*Dendropanax dentierus*	树参	L				+		
Araliaceae	*Nothopanax delavayi*	梁王茶	L				+		

Family	Species Name	Chinese name (Local Name)	Parts eat: L Fl Fr Sh Sd Ly	LD 1*	SL 2*	CN 3*	ZQ 4*	LD 5*	YX 6*
Araliaceae	*Schefflera delavyi*	鹅掌柴	L			+			
Araliaceae	*Brassaiopsis angustifolia*	柏那参	Fr/L				+		
Araliaceae	*Brassaiopsis fatsioides*	罗伞 (HT)	L						+
Anacardiaceae	*Rhus chinensis*	盐肤木#	Ly					+	
Apocynaceae	*Melodinus khasianus*	景东山橙#	Fr?						
Papilionaceae	*Ormosia olivacea*	榄绿红豆（大树豆）#	Sd					+	
Myricaceae	*Myrica esculenta*	毛杨梅#	Fr				+	+	
Aquifoliaceae	*Ilex Szechwanensis*	川冬青#	Fr?						
Aquifoliaceae	*Ilex polyneura*	多脉冬青#	F					+	
Aquifoliaceae	*Ilex macrcarpa*	大叶冬青	L			+			
Aquifoliaceae	*Ilex microparpa*	小叶冬青	L			+			
Vitaceae	*Ampelopsis delavayana*	三裂叶蛇葡萄							
Vitaceae	*Tetrastigma obtedtum*	五爪金龙					+		
Vitaceae	*Tetrostigma hypoglaucum*	狭叶崖爬藤					+		
Vitaceae	*Parthenocissus himalayana*	西南爬山虎							
Vitaceae	*Vitis*								
Vitaceae	*Ampelopsis* spp.	三裂叶蛇葡萄	Fr				+		
Fagaceae	*Lithocarpus xylocarpus*	木果石栎#			?	+			
Fagaceae	*Lithocarpus chingtungensis*	景东石栎#				+			

Family	Species Name	Chinese name (Local Name)	Parts eat: L Fl Fr Sh Sd Ly	LD 1*	SL 2*	CN 3*	ZQ 4*	LD 5*	YX 6*
Fagaceae	*Castanopsis. Orthacantha*	元江栲#	Sh					+	
Fagaceae	*Castanopsis wattii*	腾冲栲#	Fr			+			
Theaceae	*Ternstroemia gymnanthera*	厚皮香#	L			+			
Theaceae	*Eurya semiserrulata*	半齿柃	?						+
Theaceae	*Hartia sinensis*	舟柄茶#	L/Fl			+			
Theaceae	*S. noronhae*	滇木荷#	L			+			
Salicaceae	*Populus bonatti*	滇山杨#	L			+			
Styracaceae	*Styrax perkinsiae*	安息香#	L			+			
Symploceae	*Symplocos botryanthes*	总状山矾	Fr/L			+			
Symploceae	*S. ramosissima*	多花山矾	L			+			
Proteaceae	*Helicia nilagirica*	母猪果	Fr				+		
Euphorbiaceae	*Mallotus philippinensis*	粗糠柴#	?					?	
Euphorbiaceae	*Phyllanthus emblica*	余甘子 (HT)	Fr				+		+
Euphorbiaceae	*Glochidion wrightii*	白背算盘子 (HT)	Sd						+
Polygalaceae	*Polygala arillata*	黄花远志#	Fr				+		
Urticaceae	*Debregeasia edulis*	长叶水麻	Fr				+		
Campanulaceae	*Campanumoea javanica*	大花金线	Fr				+		
Campanulaceae	*Gynostemma pentaphyllum*	绞股兰	Ly/Sh	+					
Moraceae	*Morus alba*		Fr				+		
Melastomaceae	*Melastoma normale*	展毛野牡丹	Fr				+		
	Artocarpus chaplasha		Fr				+		
	Vibernum (2spp)	臭荚迷 水红木	Fr				+		

Family	Species Name	Chinese name (Local Name)	Parts eat: L Fl Fr Sh Sd Ly	LD 1*	SL 2*	CN 3*	ZQ 4*	LD 5*	YX 6*
Juglandaceae	*Juglans cathayensis*	核桃	Fr				+		
Rubiaceae	*Psychotria yunnanensis*	九节属	Fr				+		
	Ramarina spp.		?				+		
Aristolochiaceae	*Aristolochi* spp	马兜铃	L				+		
Araliaceae	*Acanthipopanax evodiaefolius* var. *Gracilis*		L				+		
Caprifoliaceae	*Lonicera* spp.	忍冬	Fr				+		
	Helwingia (2 spp.)		L				+		
Smilacaceae	*Smilax* (2 spp.)	拔契	Fr/L				+		
Pinaceae	*Pinus armandii*	松	Sd				+		
Vittariaceae	*Vittaria flexuosa*	书带蕨	L					+	
Polypodiaceae	*Lepisorus thunbergianus*	瓦韦	L					+	

APPENDIX II. DATA SET OF HYLOBATIDS USED FOR COMPARISON (CHAPTER 8) AND MODEL CONSTRUCTION (CHAPTER 9)*.

Code	Species	Body weight (kg)	Latitude	Altitude (mm)	Temperature (℃)	Temperature variation	Minimum temperature	Maximum temperature	Rainfall (mm)	Z^a
1	*H. moloch*	5.85	6.75	50	.	.	.	.	.	.
2	*H. klossii*	5.8	1.4	80	26	10	21	31	4217	.
3	*H. muelleri*	5.75	0.4	165	.	.	.	.	2177	.
4	*H. agillis*	5.85	4.12	512.5	28	10	23	33	1219	.
5	*H. pileatus*	5.75	13	320	24	.	.	.	1847	.
6	*H. hoolock*	6.7	23.83	240	22	.	.	.	1582	.
7	*H. hoolock*	6.7	25.5	667.5	22.5	29	8	37	460	.
8	*H. hoolock*	6.7	24	.	22	22	10	32	2586	0.87
9	*H. concolor*	6.3	19.1	1000	19.6	27	.	.	1621	0.87
10	*H. concolor*	6.3	24.3	2250	12.8	28.8	−3.3	25.5	2257	0.84
11	*H. concolor*	6.3	24.3	2250	12.8	28.8	−3.3	25.5	2257	0.84
12	*H. concolor*	6.3	24.5	2450	10.1	31.4	−6.2	25.2	2254	0.83
13	*H. lar*	5.5	2.6	64	27	.	.	.	3236	0.75
14	*H. lar*	5.5	4.17	300	.	.	.	.	2207	0.91
15	*H. lar*	5.5	3.72	46	29	18.5	19.5	38	1583	0.88
16	*H. lar*	5.5	3.72	46	29	18.5	19.5	38	1982	0.89
17	*H. lar*	5.5	3.67	350	25.5	17	17	34	3229	0.91
18	*H. lar*	5.5	3.67	350	25.5	17	17	34	3400	.
19	*H. syndactylus*	10.75	3.72	46	29	18.5	19.5	38	2120	0.88
20	*H. syndactylus*	10.75	3.72	46	29	18.5	19.5	38	1982	0.89
21	*H. syndactylus*	10.75	3.75	594.5	24.5	17	16	33	2413	0.9
22	*H. syndactylus*	10.75	3.67	350	25.5	17	17	34	3229	0.91
23	*H. syndactylus*	10.75	3.67	350	25.5	17	17	34	3400	.

Code	Species	Fig tree density (n/ha)	No. of primates	Biomass of primates	Other hylobatids	Population density (n/ha)	Group density (g/ha)	Group size	Biomass (kg)
1	*H. moloch*	2.1	.	.	No	8.9	2.7	3.3	41.3
2	*H. klossii*	.	2	115.1	No	30	7.3	4.1	127.8
3	*H. muelleri*	3.3	4	277.4	No	10.2	3	3.4	45.9
4	*H. agillis*	1.2	2	.	No	18.9	4.3	4.4	79.1
5	*H. pileatus*	.	.	.	No	23	6.4	3.6	101.1
6	*H. hoolock*	.	4	.	No	0.3	0.1	3	1.7
7	*H. hoolock*	.	4	.	No	9	3	3	49.8
8	*H. hoolock*	.	4	.	No	.	.	3.2	.
9	*H. concolor*	.	.	.	No	1.7	0.4	4.3	7.8
10	*H. concolor*	1.5	2	.	No	1.35	0.45	3	15.3
11	*H. concolor*	1.5	2	.	No	.	0.35	5	.
12	*H. concolor*	0	2	.	No	4.26	1.06	4	17.02
13	*H. lar*	.	2	.	No	5.6	1.7	3.3	24.5
14	*H. lar*	2	4	256.2	No	8.3	2.5	3.3	36
15	*H. lar*	10.4	4	.	Yes	3.3	0.8	4.1	11.8
16	*H. lar*	10.4	4	866.5	Yes	7.2	1.8	4	29.2
17	*H. lar*	14.7	5	750.9	Yes	10.8	2.4	4.5	42
18	*H. lar*	9	5	750.9	Yes	.	.	.	.
19	*H. syndactylus*	10.4	4	.	Yes	3.8	1	3.8	30.7
20	*H. syndactylus*	10.4	4	795.1	Yes	12.4	3.1	4	98.3
21	*H. syndactylus*	1.5	.	.	Yes	4.7	1.2	3.9	37.4
22	*H. syndactylus*	14.7	5	675.4	Yes	15.1	3.6	4.2	117.7
23	*H. syndactylus*	9	5	675.4	Yes	.	.	.	.

Code	Species	Feed proportion (%)	Move proportion (%)	Rest proportion (%)	Singing proportion (%)	Social proportion (%)	All fruit (%)	Non-fig fruit (%)	Fig in diet (%)
1	*H. moloch*	67	20	.	.	.	61	.	.
2	*H. klossii*	.	.	.	.	.	.	.	.
3	*H. muelleri*	41	11	44	4	.	62	38	24
4	*H. agillis*	53	11	29	8	.	58	41	17
5	*H. pileatus*	26	25	37	4	8	71	45	26
6	*H. hoolock*	50	.	.	.	.	40	.	.
7	*H. hoolock*	60	15	8	2	15	65	39	26
8	*H. hoolock*	39	25	26	4	6	89	51	38
9	*H. concolor*	.	.	.	.	.	.	.	.
10	*H. concolor*	33	14	45	3	5	.	.	.
11	*H. concolor*	34	22	30.8	7.6	5.6	46.2	.	.
12	*H. concolor*	19	28	39	1	13	24	24	0
13	*H. lar*	29	47	7	2	4	62	.	.
14	*H. lar*	8	16	62	14	.	77	50	27
15	*H. lar*	42	32	.	.	.	60	.	.
16	*H. lar*	42	32	20	3	3	50	28	22
17	*H. lar*	.	.	.	.	.	56	30	26
18	*H. lar*	34	16	45	3	2	71	26	45
19	*H. syndactylus*	58	18	23	.	.	22	10	12
20	*H. syndactylus*	50	22	25	1	2	36	14	22
21	*H. syndactylus*	53	14	33	.	.	43	23	20
22	*H. syndactylus*	.	.	.	.	.	52	29	23
23	*H. syndactylus*	40	12	45	1	3	61	18	43

Code	Species	Leaves in diet (%)	Flowers in diet (%)	Arthropods in diet (%)	All fruit in minutes	Non-fig fruits (minutes)	Figs (minutes)	Leaves (minutes)	Flower (minutes)	Arthropod (minutes)
1	*H. moloch*	38	1	0	270	.	.	166	4	0
2	*H. klossii*	.	.	.	.	.	.	.	.	.
3	*H. muelleri*	32	4	2	123	76	48	64	8	4
4	*H. agillis*	39	3	1	169	120	50	114	9	3
5	*H. pileatus*	13	0	15	91	58	33	17	0	19
6	*H. hoolock*	50	10	0	108	.	.	135	27	0
7	*H. hoolock*	25	.	.	.	.	.	.	.	.
8	*H. hoolock*	6	5	.	202	115	86	13	11	0
9	*H. concolor*	.	.	.	.	.	.	.	.	.
10	*H. concolor*	.	.	.	.	.	.	.	.	.
11	*H. concolor*	46.91	5.6	0.14	70	.	.	89	9	.
12	*H. concolor*	54	6	14	.	.	.	.	.	.
13	*H. lar*	28	10	0	105	.	.	47	17	0
14	*H. lar*	12	8	2	.	.	.	.	.	.
15	*H. lar*	30	1	9	130	.	.	65	2	20
16	*H. lar*	29	7	13	112	63	49	65	16	20
17	*H. lar*	34	.	.	.	.	.	.	.	.
18	*H. lar*	4	1	24	.	.	.	.	.	.
19	*H. syndactylus*	65	9	2	85	39	47	252	35	8
20	*H. syndactylus*	43	6	15	107	41	65	127	18	44
21	*H. syndactylus*	52	6	2	138	74	64	167	19	6
22	*H. syndactylus*	40	.	.	.	.	.	.	.	.
23	*H. syndactylus*	16	1	21	.	.	.	.	.	.

Code	Species	Activity period (minutes)	Day journey length (m)	Encounters (n/day)	Song (n/day)	Territory (ha)	Territory (ha/kg)
1	*H. moloch*	660	1400	0.08	0.6	16.4	1.1
2	*H. klossii*	795	.	0.08	0.24	11	0.6
3	*H. muelleri*	486	850	0.08	1.03	39	2.3
4	*H. agillis*	550	1335	0.69	1.45	22	1.5
5	*H. pileatus*	492	833	0.45	0.6	27	1.9
6	*H. hoolock*	540	600	.	.	.	.
7	*H. hoolock*	.	.	.	.	31	1.9
8	*H. hoolock*	581	1100	.	1.3	32	2.2
9	*H. concolor*	.	.	.	.	.	.
10	*H. concolor*	.	.	.	.	.	.
11	*H. concolor*	501	838.7	0	0.4	.	.
12	*H. concolor*	509	1306	.	0.43	.	.
13	*H. lar*	584	1600	0.05	0.85	29.4	2
14	*H. lar*	.	.	.	0.54	13.6	1.2
15	*H. lar*	516	1670	.	0.73	.	.
16	*H. lar*	533	1521	0.16	.	.	.
17	*H. lar*	630	1250	.	0.42	34	1.9
18	*H. lar*	573	.	.	.	.	.
19	*H. syndactylus*	665	969	0	0.33	26	0.73
20	*H. syndactylus*	591	723	0	.	.	.
21	*H. syndactylus*	630	800	0.3	0.23	14	0.4
22	*H. syndactylus*	.	748	.	0.27	16	0.5
23	*H. syndactylus*	601	.	.	.	.	.

Code	Species	Home range (ha)	Home range (ha/kg)	Overlap proportion (%)	Sources
1	*H. moloch*	17.4	1.1	6	Kappeler(1984)
2	*H. klossii*	.	.	.	Tilson(1981),Tenaza(1975)
3	*H. muelleri*	44	2.6	11	Leighton(1987)
4	*H. agillis*	29	1.9	24	Gittins(1980, 1982)
5	*H. pileatus*	36	2.5	25	Srikosamatara(1984)
6	*H. hoolock*	350	21.1	.	Mukherjee(1982, 1984)
7	*H. hoolock*	.	.	.	Alfred and Sati(1986, 1990)
8	*H. hoolock*	35	2.4	8	Islam and Feeroz(1992)
9	*H. concolor*	362.5	19.2	.	Liu et al(1989)
10	*H. concolor*	.	.	.	Lan (1989, 1993)
11	*H. concolor*	55	.	.	Present study
12	*H. concolor*	87	5.4	.	Chen (1995)
13	*H. lar*	39	2.7	26	Ellefson(1974)
14	*H. lar*	18	1.5	24	Johns(1986)
15	*H. lar*	55	3.3	.	Chivers(1974)
16	*H. lar*	57	3.8	.	Raemaekers(1979)
17	*H. lar*	40	2.3	15	Rijksen(1978)
18	*H. lar*	.	.	.	Palombit(1997)
19	*H. syndactylus*	34.2	1	.	Chivers(1974)
20	*H. syndactylus*	47	1.5	.	Raemaekers(1979)
21	*H. syndactylus*	14.7	0.5	15	Chivers(1974)
22	*H. syndactylus*	21	0.6	25	Rijksen(1978)
23	*H. syndactylus*	.	.	.	Palombit(1997)

*a, Index of rainfall diversity.