GIBBON LOCOMOTION IN DISTURBED PEAT-SWAMP FOREST, SEBANGAU, CENTRAL KALIMANTAN

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Bornean agile gibbon (*Hylobates albibarbis*) feeding in the canopy

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PREFACE

I declare that this dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically stated in the text. The work described in this thesis was conducted from the Wildlife Research Group, The Anatomy School, University of Cambridge, U.K under the supervision of Dr. D. J. Chivers. The text (excluding tables and figures) does not exceed the word limit, of 15,000 words, for the respective Degree Committee.

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SUMMARY

The effects of habitat disturbance were carried out on a recently-habituated population of Bornean agile gibbons (*Hylobates albibarbis*). Aspects of their locomotor behaviours were investigated in varying levels of disturbance and assessed in relation to various social and morphological factors. The study was carried out from September 2005 to June 2006 in Sebangau National Park, Central Kalimantan, Indonesia. The National Park is believed to hold around 30,000 individuals, which is thought to be the largest remaining population of Bornean agile gibbons in the world.

Peat-swamps are very important gibbon habitats and this was the first study of its kind in this habitat type. The disturbance in the area made it relatively distinct, in that it provided the gibbons with an uneven canopy for travel. Comparisons were made between the use and availability of forest types and canopy heights for travel and predictions were formulated regarding the outcomes of these. It was discovered, as expected, that gibbons appear to favour better forest types over worse and higher canopy heights over lower. As gibbons are a highly arboreal species, they require certain habitat criteria that suit their specific needs. They are adaptable in the sense that they can survive in disturbed areas but what remains unknown is under what level of pressure this is putting the population in the long term. Forest disturbance of up to ten years is shown to cause a change in the locomotor behaviour of gibbons and regeneration, in particular, to have a worse effect than gap areas, due to the formation of a highly-uneven canopy. The frequency of coming to the ground in order to cross gaps is related to energy expenditure; travelling the least effective route possible will expend more energy than travelling in a direct line. Gibbon locomotion is also based on energy loss and gain, some modes of travel being more efficient than others. It was seen here that gibbons are counter-acting the energy lost during travel in uneven canopy layers by exhibiting a specialised mode of travel – brachiation - thus suggesting that this form of locomotion is more energy-efficient than jumping, which they appeared to favour in all other forest types. Brachiation is a key feature of this socially monogamous, territorial species, as it enables them to exploit a wide-range of food sources across a large home range. It is suggested in this study that brachiation also acts as a means of reducing the energetic cost of travel.

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My sincere thanks to everyone I met and worked with in Borneo and making my time there so special. Especially to Ellie Monks, my best friend who was tireless in amusing me and keeping my spirits up when the gibbons had gone into hiding. Without her support I wouldn't have come so far. To 'the boys', Ari, Coes, Twenty, Thomas, Santi, Zery, Yudhi, Iwan, Dewa, Yon, Eben, Upik, Kris Yoyo, Hendri, Idrus and Karno who all had a hand at some point in collecting my data. I thank them so much for everything, looking after me in the forest, teaching me about their culture, making me laugh and playing such good guitar. To the staff at camp, in particular Ibu Yanti. I have never met such a hard-working lady and am so grateful to her for the 'telor goreng' every morning before dawn. To all the field assistants who worked alongside me, Laura Graham, Angie Benton-Brown, Kirsty Tuson, Marc burung, Katie Brady and Anthony Lusher. My time in Borneo would not have been what it was without them.

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CHAPTER 1 – INTRODUCTION

1.1 Evolution and Taxonomy

1.1.1 Species History

Humans, the great apes and the small apes (Hylobatidae) comprise the super-family of Hominoidea. There are believed to be twelve or more gibbon species in existence (Geissmann 2002; Muller *et al.* 2003; Takacs *et al.* 2005), although published work on gibbon phylogeny is inconsistent. Whilst the larger apes are our closest-living relatives, gibbons are not far behind (Muller *et al.* 2003). Thus, it is surprising to find that information regarding their evolution, taxonomy and phylogeny is still under debate. There are very few records of gibbon fossils (Geissmann 2002a). The earliest gibbon-like fossils (*Propliopithecus*) were said to date back to the Miocene era (5-23 million years ago) and were found in Africa and Europe. There have yet to be any discoveries from the Pliocene era (1.8-5 million years ago), even in Asia (Fleagle 1988; Chivers 1977). As a consequence of the lack of information regarding fossil evidence, gibbon evolution can mainly be constructed by modern-day gibbon characteristics, such as hair colour, vocal repertoires, morphology and molecular data. In a study by Geissmann (2002), these data, when analysed, all came up with slightly different interpretations of phylogeny. The non-communicatory data were originally regarded as being the most suitable means of reconstructing phylogeny, but it is shown in Geissmann's (2002) study that, of the data sets used, vocal data were the most reliable, with hair colour being useful only for distinguishing between subspecies.

Napier and Napier (1967) separated gibbons into two sub-genera; the *Symphalangus* (siamang) and *Hylobates* (all other small apes). Groves (1972) suggested one genus (*Hylobates*), with three sub-genera: (1) *Nomascus*, containing *H. (N.) concolor* which has six sub-species; (2) *Symphalangus,* containing *H. (S.) syndactylus* which has two sub-species; and (3) *Hylobates,* containing four species – *H. klossii* (monotypic), *H. hoolock* (two sub-species), *H. pileatus* (monotypic) and *H. lar* (eight sub-species). All these species are listed on CITES Appendix I (2006), emphasising the urgent need for their conservation.

Although taxonomy is always a subject of great debate, it is generally accepted that there are four distinct sub-divisions in which small apes should be categorised: the sub-genera *Bunopithecus, Hylobates, Symphalangus* and *Nomascus* (Figure 1.1). All present gibbon species are said to have diverged over a relatively-short evolutionary time period. The various contradictory beliefs about gibbon phylogeny suggest that the evolutionary time period of divergence being so short could indicate that they have not yet accumulated enough genetic variation to warrant separate species/sub-species distinction (Muller *et al.* 2003). Geissmann (1993) stated that the first divergence was from *syndactylus,* the *concolor* group, or a shared ancestor. This information is contradictory however, to various other publications (Muller *et al.* 2003), which suggest *Bunopithecus* (*Hoolock*) to have been the first to diverge, followed by *Hylobates,* with *Symphalangus* and *Nomascus* the last to diverge. Again, other opinions (Takacs *et al.* 2005) stated either *Bunopithecus* or *Nomascus* to be the most basal, with *Hylobates* the most recent divergence. Taxonomic classifications are still under scrutiny by scientists, but the trend is to recognise four genera.

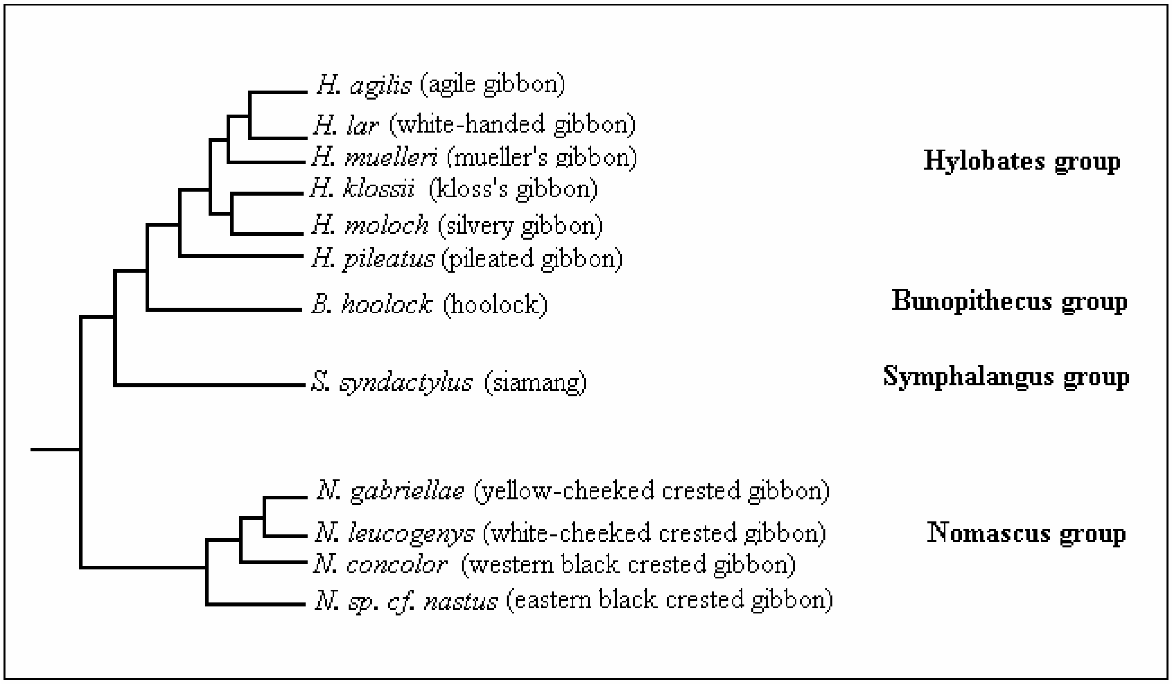


Figure 1.1 Preliminary phylogenetic tree of the twelve gibbon species based on the combined data of vocal and molecular studies (Geissmann 2002; Roos and Geissmann 2001)

Some authors believe that *Hylobates albibarbis* is morphologically more similar to *H. muelleri* (although not identical) than to *H. agilis* (Leighton 1986), but the calls of *H. albibarbis* are more strikingly similar to *H. agilis,* compared to *H. muelleri* (Groves 1984; Marshall and Sugardjito 1986). It was suggested that *H. albibarbis* should become a subspecies of either *H. muelleri* or *H. agilis*, but this could give rise to issues regarding morphology being more important than calls in taxonomy, or *vice versa.* Two plausible solutions have been proposed: (1) separate *H. albibarbis* as a species of its own, which would give the two criteria equal weight, or (2) combine *H. agilis, H. albibarbis* and *H. muelleri* into one species, which would also give the two criteria equal weight (Groves 1984). After more detailed evidence revealed a similarity in hair characteristics between the species (Geissmann 1993), it was concluded that the first option was the most reasonable.

In a study by Groves (2001), the Bornean agile gibbon (*H. albibarbis)* was classified as a separate species, and no longer a subspecies of *H. agilis.* These findings arose from a variety of research on the vocal (Geissmann 1995), morphological (Groves 2001) and genetic characteristics (Garza and Woodruff 1992) of the species. *H. albibarbis* are classed as Lower Risk/Near Threatened on IUCN Red List of Threatened Species (Eudey 1994).

1.1.2 Distribution

The four sub-genera of gibbons are widely distributed throughout South-east Asia, as shown in Figure 1.2.

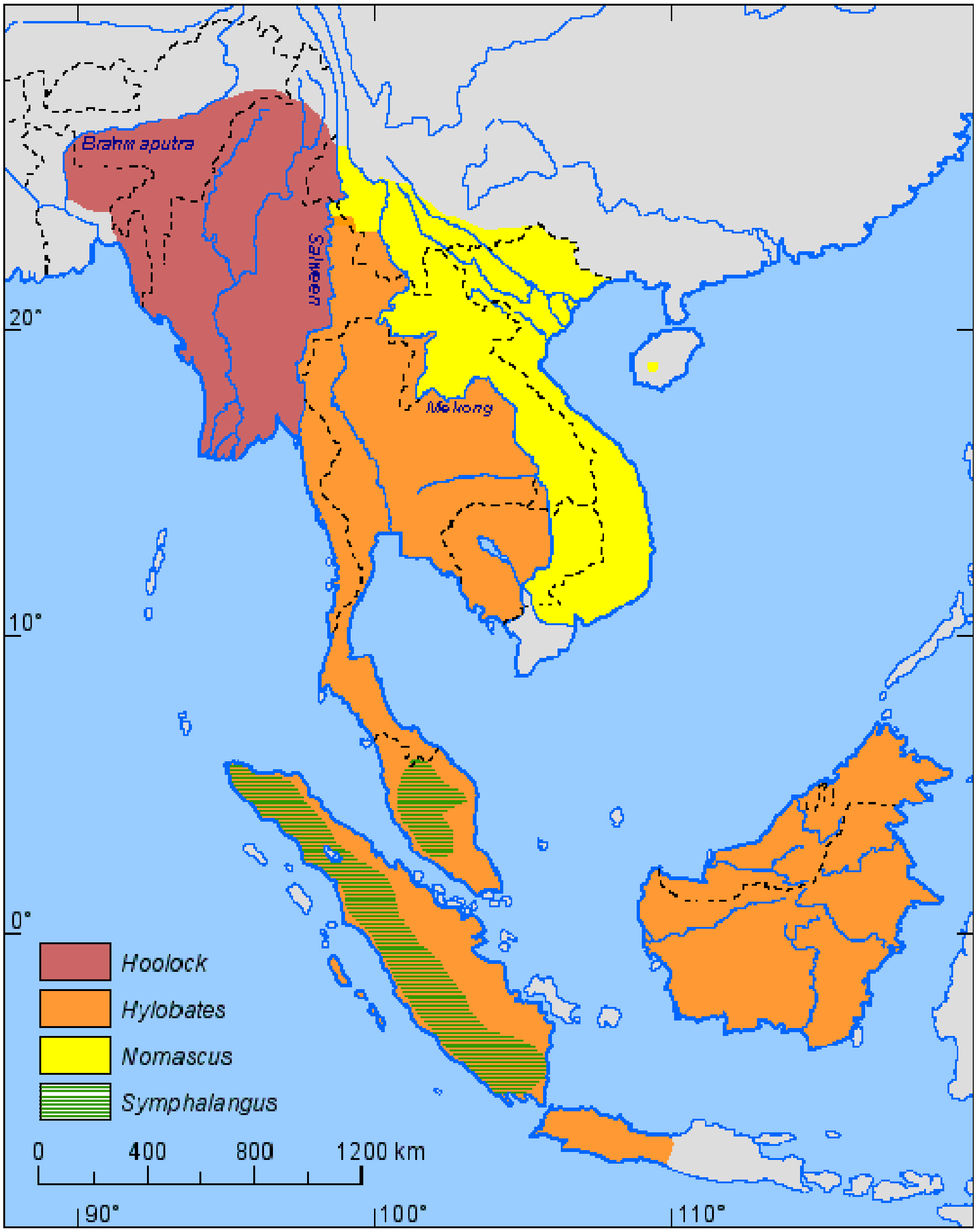


Figure 1.2 Distribution of the four gibbon subgenera (Geissmann Research website 2000)

H. albibarbis occur only in Central Kalimantan, south of the Kapuas and west of the Barito rivers, as shown in Figure 1.3 (Chivers 1977).

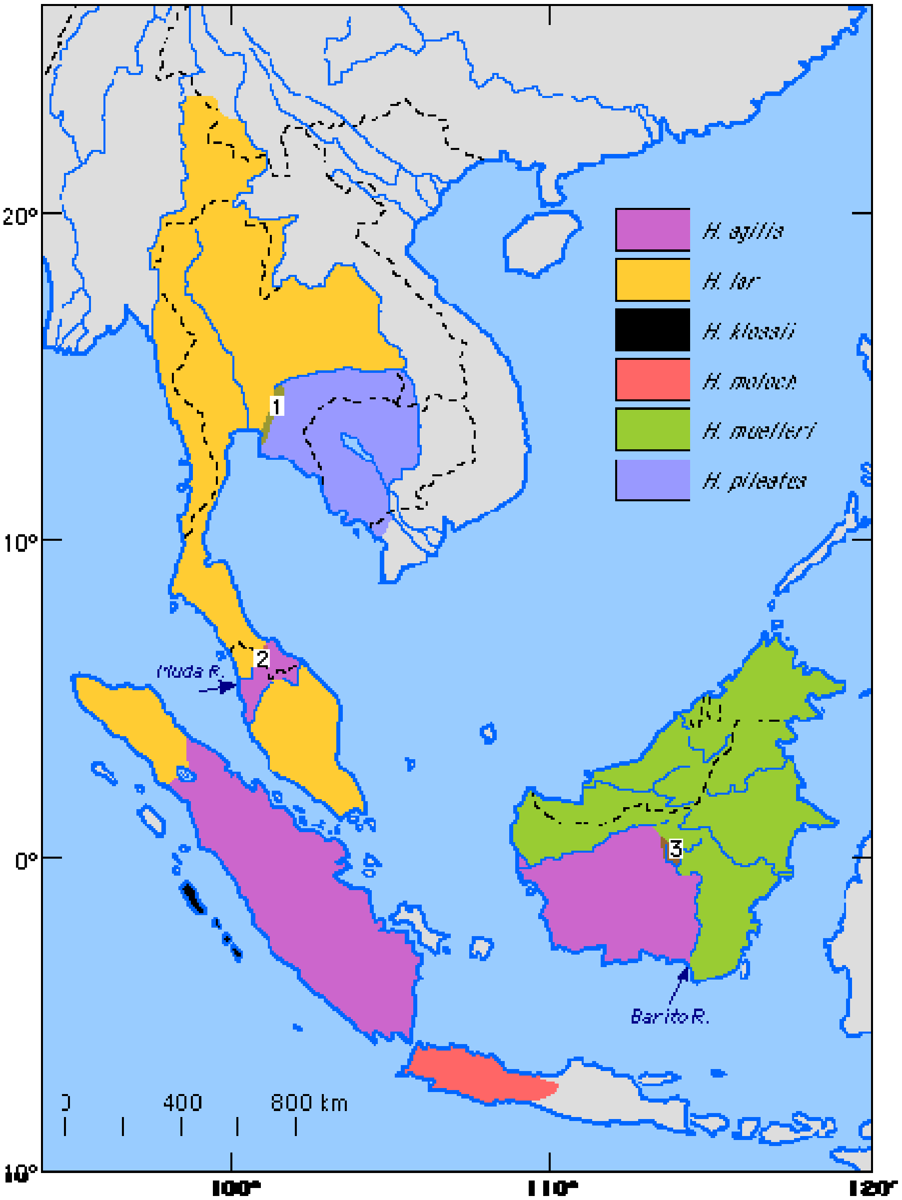


Figure 1.3 Distribution of the subgenus *Hylobates* across S.E Asia showing the three areas of hybridisation (Geissmann Research website). The number 3 indicates the area of hybridisation between *H. muelleri and H. agilis*

1.2 Socio-ecology

1.2.1 Social structure

Gibbons can be identified as territorial, monogamous, frugivorous, duetting and suspensory (Chivers 1977; Preuschoft *et al.* 1984). They are small, brachiating apes, living at low biomass density and defending small territories against conspecifics (Leighton 1986; Chivers 2000). They are highly mobile in the forest, using brachiation as their main form of locomotion when moving in the upper canopy. This adaptation provides them with a swift and direct movement, enabling them to exploit scattered food sources and defend a large territory (Gittins 1983).

Carpenter (1940) was the first to observe the co-dominant, monogamous social groups in which gibbons lived. Subsequent studies (Ellefson 1974; Chivers 1974) have supported his observation of groups consisting of a mated pair with up to 4 offspring. Monogamy in primates is restricted to those who are arboreal, frugivorous and territorial, e.g. gibbons, indris, tarsiers and some species of marmosets. It is a strategy that minimises foraging efforts, food and sexual competition, and reproductive waste, but can leave gibbons susceptible to changes in their environment (MacKinnon and MacKinnon 1984). Morino and Ulrich (2004) suggest two hypotheses for the evolution of their social monogamy. The first being the infanticide-protection-hypothesis, meaning that males will provide protection for their offspring, which balances out the mating opportunities lost through monogamy. The second being the mate-guarding-hypothesis, meaning that it is less costly to the male to protect and mate with just one female, rather than expend energy mating with multiple females.

With no solid evidence of birth seasonality (Leighton 1986) and birth-intervals of two to three years (Mitani 1985; Geissmann 1993), there are normally only two immature offspring present in the group, and only ever one representative of an age group at any one time (Chivers 1984). When the adolescents become sexually mature, they will leave the natal group in search of a mate, especially if they are male. The age classes have been described by Leighton (1986); infant – 0-2/2.5yrs, juvenile – 2-4yrs (dependent on level of independent locomotion), adolescent – 4-6yrs (not yet fully grown), sub-adult – 6-8 (adult sized, but yet to have paired off) and adult – 8+ (fully grown and able to reproduce). Carpenter (1940) was the first to classify individuals into age categories, but these were designed mainly for instantaneous recognition rather than gauged over a long developmental period. The age categories, mainly based on differences in behaviour and body size, are shown in Table 1.1.

Table 1.1 Definition of age-class by Palombit (1992)

Infant	Regularly suckling from the mother, being fully or partially dependent on her for travel and when older, getting playful with all individuals in the group.
Juvenile	Immature individuals that are not of adolescent size but travel independently from their mother, though still get assistance from adults when encountering large gaps.
Adolescent	Larger than juveniles, yet still immature in the features, with the canines not being fully developed. Locomotion is entirely independent and frequent play behaviour occurs.
Sub-adult	Yet to pair off with a mate, though of adult body size. Difficult to identify in males but easy in females with their noticeable non-pendulous nipples.
Adult	Paired to another individual of the opposite sex, duets with the mate in loud calls, defends a territory and reproduces.

1.2.2 Calls

All gibbon species produce long, loud and complex song bouts at particular times of day, usually in the early morning. These calls are usually sung from tall, emergent trees, thus enabling the song to carry through the canopy as far as possible (Marshall and Marshall 1976; Haimoff 1984a,b; Cowlishaw 1992, 1996; Geissmann 1993; Dallmann and Geissmann 2000). The calls are known to contain strong evidence of species- and sex-specific characteristics (Tenaza 1985; Geissmann 2000; Dallmann and Geissmann 2000, 2001).

The similarities in song between species indicate that they all shared a common ancestor. They produced duets that probably evolved from a song common to both sexes that later became separated into male/female specific parts (Geissmann, 1993, 2002).

Most species call in the form of well-coordinated duets; in *Hylobates klossii* and *H. moloch* duetting is absent, but female solo songs are common (Geissmann 2002b).

Duets in agile gibbons are structured into three distinctive sequences 1) the introductory sequence, occurring at the start of the song bout, followed by 2) the organising, 3) the great-call sequences, which are produced in irregular alternation throughout the remaining song bout and 4) the post-climax sequence. Duet bouts of all species are produced and organised in this particular way, with the least unpredictable and most obvious characteristic being the female great-call (Haimoff and Gittins 1984).

There are five main sections of phases, shown in Figure 1.4, comprising the great-calls of the agile gibbon females; these include the introductory, inflective, climax, post-climax and terminal phases (Haimoff and Gittins 1984).

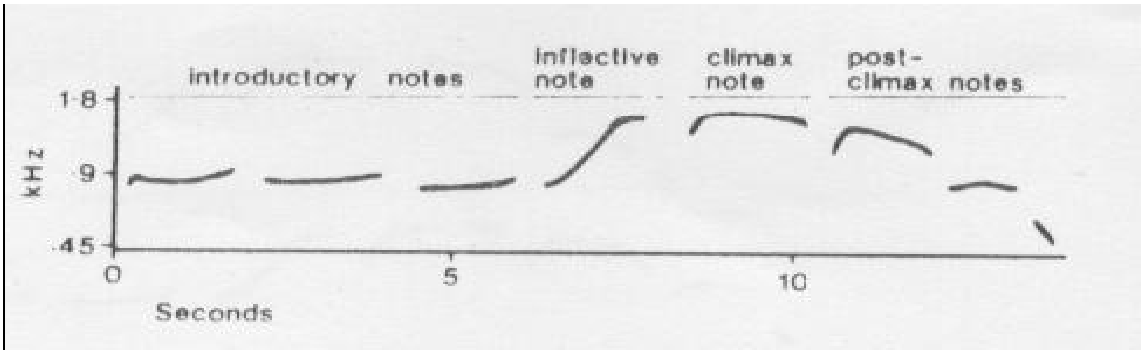


Fig 1.4 The five main phases of a female agile gibbon’s great-call (Haimoff and Gittins 1984)

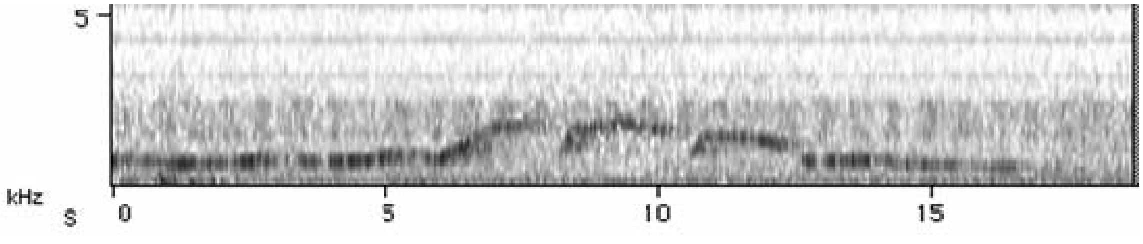


Fig 1.5 Recordings of female great-calls from Sebangau study area (Thompson 2004)

Calls can typically be heard up to 2km away (depending on the topography of the area) and range from 0.2 – 5 kHz in frequency, which will vary between species

(Geissmann 1993). The study individuals in Sebangau were observed to range roughly between 0.4 – 1.9 kHz (Figure 1.5) (Thompson 2004; Cheyne 2004).

All gibbon species have call sequences of different frequencies and phrases that are diagnostic of each species (Haimoff 1984a). Haimoff and Gittins (1984) state that one function of gibbon song is for inter-group communication; selecting for and favouring individual recognition within an area. Individual-call characteristics are one of the main mate-choice criteria; this reduces the likelihood of inbreeding through recognition of family-specific calls. Playback experiments have been carried out on various bird species, which recognise, and occasionally respond to, the songs of other species, such as closely-related competitors (Catchpole and Slater 1995). They are also able to learn the songs of their neighbours and distinguish between unfamiliar individuals of the same species and neighbours. This suggests that song has a broad range of functions and assists recognition of a diversity of significant criteria, including: sex, kin, species, mate and other individuals, such as territorial neighbours.

1.2.3 Function of calls

As gibbons are socially-monogamous species, they use songs as a way of ensuring exclusive reproductive access to their mate (although this is currently a subject under debate and genetic studies are needed to check its validity), maintaining pair bonds, and also to defend their territory against conspecifics (Carpenter 1940; Ellefson 1968; MacKinnon and MacKinnon 1984; Leighton 1986; Cowlishaw 1992, 1996). As aggressive inter-group encounters on the boundaries of territories are uncommon, it is unsure whether the use of loud songs is specifically intended for territory or mate defence (Brockelman and Srikosamatara 1984). It is generally assumed that it is a combination of the two. Raemaekers and Raemaekers (1984) support this and conducted a study on vocal interaction, whereby playback experiments of the ‘ooaa’ duet were carried out on lar gibbons. They suggest that duetting functions for both between-group territoriality and inter-group bonding. Mitani (1987) concurs with this study and also conducted playback experiments in order to assess the behaviours agile gibbons exhibited to uphold monogamy and territoriality. He concluded that males are inhibited from becoming polygynous by female territoriality. Overall, the main objective of producing loud, elaborate songs is to advertise an individual's presence in an exclusively-defended territory (Haimoff and Gittins 1984).

The use of loud, elaborate calls for mate advertisement or territory defence is reinforced typically by complementing the display with a visual component (Mitani 1985). Characteristically, at the climax note of the female's great-call, the gibbons will exhibit a vigorous acrobatic display, branch shaking, the breaking and throwing of dead branches and brachiating fast around the tree (Chivers 1974; Geissmann 1993). This is another way of demonstrating strength and aggression to conspecifics in the area.

In a study by Mather (1992), in which newly-mated pairs of the hybrid species (*H. albibarbis* x *muelleri*) were observed to sing more frequently in order to synchronise duetting, as it is more difficult for unfamiliar individuals to adjust to each other's idiosyncrasies. As they sung more frequently, their energy was spent on that, rather than on copulation, thus, lowering the birth rate of the species. Alternatively, when nutritious food is abundant both singing and copulation can increase, thus sustaining the birth rate (Chivers 1974). Duetting can indicate how well established is the pair, thus, males are less likely to invade a territory if the mated pair sounds well established (Chivers 1984; Cowlishaw 1992).

Individuality also plays in important role in maintaining good communication with groups inhabiting a population. It is believed that individuality has been genetically selected in gibbon song. This provides advantages, such as the ability to communicate effectively with individuals inhabiting the same area, the ability to detect alarm calls, and the ability to differentiate between calls needing a vocal response or not (Haimoff and Gittins 1984). The female great-call is the most stereotypic part of the song, hence the best place to look for differences in variation between individuals, and between populations (Haimoff and Tilson 1985; Dallmann and Geissmann 2000, 2001).

1.2.4 Morphology

Gibbons are the smallest of all the apes, weighing, on average, about 5kg. The hoolock are slightly heavier at 6-8kg and the siamang is twice is heavy, weighing 10-12kg (Leighton 1986). Colour is highly variable, some species being sexual dichromatic (*H. concolor, hoolock* and *pileatus*), some being monochromatic (*S. syndactylus, H. moloch* and *H. klossi*), and some being polychromatic (*H. muelleri, agilis* and *lar*) (Chivers 1977). *H. albibarbis* is polychromatic, with colours ranging from dark browns to pale tan colours as shown in Figures 1.6 and 1.7 (per. obs. 2005).

Long arms relative to body size enable dexterity and allows for efficient brachiation, whereas moderately long leg-to-body-size ratio has allowed for bipedalism.

Figure 1.6 Adult male

Figure 1.7 Adult female (with ventral infant)

1.2.5 Activity patterns

Gibbons are frugivorous, their diet consisting mainly of ripe fruits, figs (*Ficus* spp.) and leaves (Gittins and Raemaekers 1980). Activity patterns of the gibbons are unusual amongst other primate species. They are normally active for about 8-10 hours a day, arising before dawn and going to sleep long before sunset (Leighton 1986; Chivers 1984). Data from Chivers (1984) show agile gibbons to spend between 3 and 4 hours feeding each day (mostly in the morning), the rest is spent resting, interacting socially or travelling. For agile gibbons, travelling takes up a significant proportion of the day, as it is imperative that the individuals maintain the defence of their territory (Chivers 1984).

Gibbons are sympatric with several other primate species – orang-utans (Pongidae), the siamang (*Symphalangus syndactylus*), other gibbon species (Hylobatidae), langurs and macaques (Cercopithecidae), lorises (Lorisidae) and tarsiers (Tarsiidae). Specialised adaptations enable the gibbons to inhabit the same area, whilst efficiently exploiting scattered food sources that are unavailable to certain other species (MacKinnon and MacKinnon 1978; Raemaekers 1977).

1.2.6 Territories and home-ranges

Chivers (1984) states that, on average, gibbons have fixed home-ranges of about 34 hectares (ha) and defend 75% of this area as an exclusive territory. Sizes vary widely between different species of gibbon; the largest being that of the Müeller's in Kutai and the smallest being of the moloch in Ujung Kulon (Chivers 2000). Brockelman and Srikosamatara (1993) regard a density of less than two groups/km^2 as low. The density estimates for the study site are lower than this, at 1.72 groups/km^2 (Cheyne *et al.* in press). Obviously, home-range sizes will vary greatly, depending on the type of habitat and levels of disturbance present (Leighton 1986), and in the mixed-swamp forest (MSF) study site, large gaps in the canopy are all too common.

Territory is an area within the home-range that is used exclusively by the resident group and defended against conspecifics (Chivers 1984). Gibbons have classic territories, meaning that feeding, mating and the raising of young all occur in this defended space. The groups will travel together, or in reasonably close proximity to each other, and routinely visit areas of their home-range, perhaps every 2 to 3 days (Leighton 1986). Patrolling behaviour is not common amongst the gibbons (Gittins 1980); it is more likely that the ranges are covered in terms of food tree locations (Ellefson 1974). Gibbons living in habitats with seasonal fruiting periods will defend a large proportion of their home-range (80-90%) instead of travelling around a larger area. They get to know the locations of food sources in the long term, so cannot afford to share them with neighbours (Chivers 2000). Agile gibbons are considered to have relatively small home-ranges, in comparison with other species. The Müller/agile hybrid gibbons of Barito Ulu have home ranges of 18ha, with territory sizes of 17ha (Chivers 2000).

Cheyne *et al.* (in press) calculated an average territory size of 53ha for the gibbons present in the mixed-swamp forest (MSF) of the Sebangau study site (shown in Figure 1.8), with an average of 15% overlap with other groups' territories. This is similar to data from Chivers (1984), who states a 6% overlap of territory for Mueller/agile gibbons of Barito Ulu, which is further to the north and constitutes a hybrid of the two species. These estimates are again somewhat different from the large overlap (64%)

(which can lead to high stress levels and an increase in aggressive encounters) described by Reichard and Sommer (1997) in Khao Yai National Park. These differences again support the observations that home range and territory size can vary greatly, depending on the level of disturbance and fragmentation between different locations, as seen in Khao Yai.

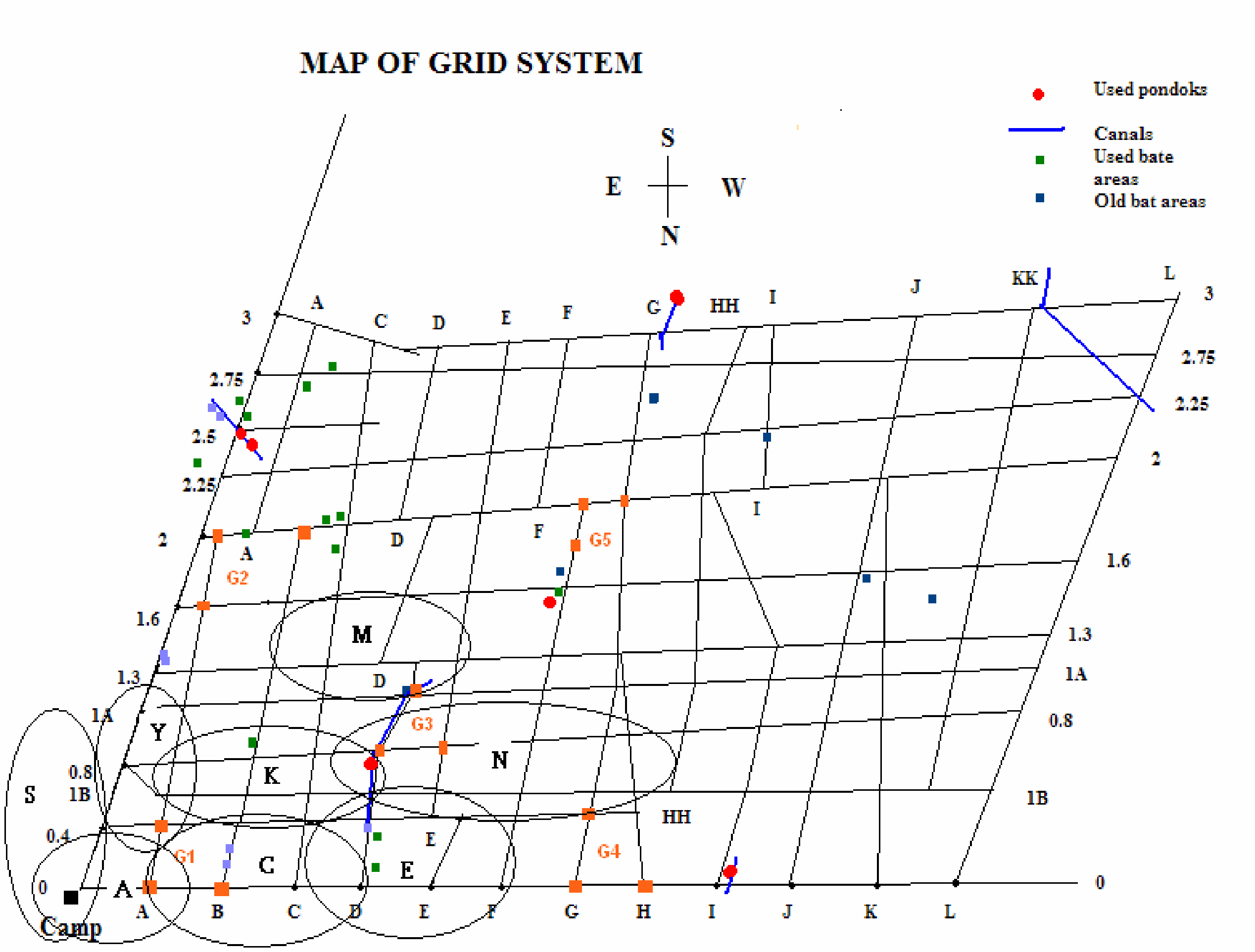


Figure 1.8 Map of the grid-system and the territories of the study groups (after Cheyne *et al.* in press) M=Manga, N=Ninja, K=Karate, E=Group E, C=Group C, Y=Yoga, A=Group A, S=Simpsons

1.3 Conservation

Gibbon populations have suffered a decline in the last 40 years, largely due to the destruction of their habitat by means of encroachment, cultivation, rubber plantations (Haimoff *et al.* 1987), fire, oil-palm plantations and, primarily, illegal logging (Chivers 1977; Leighton 1986). Other, smaller-scale reasons for their decline are due to the hunting for the illegal pet trade and also for use in traditional medicines. These problems mainly stem from human influence and encroachment into forest environments. Tropical rain-forests are found mainly in developing countries, which often make the mistake of regarding their forests as a renewable resource, or as a waste of land for agriculture or other such forms of economic value (Johns and Skorupa 1987).

1.3.1 Illegal logging

Illegal logging creates large patches of fragmented forest, in which gibbon populations cannot be expected to survive in the long term. Selective-logging has been seen as the long-term 'compromise' for both humans and animals, but areas that are set to be logged selectively are often over-exploited by the timber industries. Johns and Skorupa (1987) recommend that selective-logging practices should normally involve the felling of not more than 10% (which causes damage of up to 50%) of the trees; thus enabling the remaining trees to regenerate, and the effects of logging to be counteracted. Nevertheless, there are always exceptions to the rule and some logging operations have been recorded destroying anywhere from 5-70% of the forest, thus exceeding the average predicted level of destruction of 45-50% (Johns and Skorupa 1987). Gibbons are highly-adaptable species and can tolerate various levels of disturbance (Chivers 1974, 1977). Some habitat-disturbance studies (Johns 1983a,b; Skorupa 1986) have shown that the survival of certain primates communities can be tolerated alongside logging practices. In this study I will aim to provide insight into the actual level of disturbance it takes to render a population unsustainable.

In a personal communication to Chivers (1977), Brockelman stated that any sort of logging can have a serious negative effect on gibbon communities for several reasons, e.g. the elimination of sleeping, resting, and feeding trees, an increase of light intensity can change the entire microclimate of the forest, several food trees are shade tolerant and some species of fig trees need shade in order for the seeds to germinate successfully.

1.3.2 Protected areas

Kalimantan has few protected areas for gibbons; Tanjung Puting Reserve in the south-west, Kutai Reserve in the east (3060km^2), of which a large proportion was felled in the late 1960s and destroyed by huge fires in 1982-83 and 1997-98. Since October 2004, 5860km^2 of the Sebangau catchment was designated a National Park. Not only is it home to a vastly-diverse range of plant and animal species, it is calculated to be home to at least 30,000 gibbons (Cheyne *et al.* in press) and houses the largest continuous orang-utan population in the world, at nearly 7000, individuals (Morrogh-Bernard *et al.* 2003). Thus, it is of extreme ecological importance, and the necessity for efficient management and effective conservation practices is constantly required.

As gibbons are almost completely arboreal, this must be taken closely into account when constructing plans for the management and conservation of their habitat. Their suspensory behaviour enables them to exploit resources in terminal branches; thus, they are able to use a wide variety of tree species for food. One of the main food sources for many primates, including the small apes, are fig trees (*Ficus spp*), which are a highly adaptive, versatile genus that appears to be continuously available in all types of forest. Fig trees are even more abundant in areas of forest that have been disturbed to some degree (Corner 1952).

Looking at conservation as a whole, there are a few possible solutions to the preservation of forests. Above all, the main idea should be to focus on the peaceful coexistence of humans and forest, but this, in many cases, would be difficult to implement, and a balance must be found that is beneficial to both local people and the forest. Conservationists and logging companies must come to a compromise, where (a) some areas of forest are left untouched, (b) selected areas are cleared and used by such logging companies and (c) the principal area is managed effectively to reduce disturbance levels of the forest ecosystem, whilst generating some subsidy for the people. Logging practices and the management of buffer zones for sustainable forest produce must be controlled in order for the forests to be able to regenerate

Actions urgently need to be taken to ensure the survival of the species:

1) Quotas to be established with logging companies and introduction of sanctions if quotas are violated.
2) Establishment of protected areas and national parks where logging is stopped.
3) Enforcement of local patrol teams to police the protected areas.
4) Thorough and efficient management of forest areas, with either a ban on logging or at least controlled selective-logging practices.
5) Stronger law enforcements to minimise the illegal pet trade and the export of illegal timber.
6) Minimisation of hunting with the provision of a different source of protein.
7) Develop Environmental Impact Assessments (EIAs) and focus on research into forest ecology, eventually establishing what level of disturbance gibbons can tolerate.
8) Involvement and education of local people on how to use the forest as a natural, renewable resource and to attempt to fundamentally change attitudes towards wildlife and conservation.
9) Rehabilitation and reintroduction is a short-term solution to saving wild individuals, but focusing on the conservation of habitat in the first place would be a long-term solution to protecting wild populations.

1.3.3 Fire

Fire is one of the largest threats to the existence of tropical forests. It can cause untold levels of destruction on a vast scale if it is not properly controlled. Tropical peat-swamps provide one of the largest sources of organic carbon left on earth. The species-rich forests of Indonesia are particularly vulnerable to continuous environmental change by means of habitat degradation, both legal and illegal logging, and drainage of the peat domes by logging canals. The consequences of these changes are affecting the forests' stability and making them particularly susceptible to forest fires (Watson *et al.* 2000; D'Arcy and Page 2002). In the long term, forest fires inhibit regeneration by means of destroying seed banks (Uhl *et al.* 1981), reducing soil fertility and destroying plants that would later aid regeneration (D'Arcy and Page 2002).

When the peat burns, a carcinogenic haze is produced from the release of large quantities of fine matter (Page *et al.* 2002). This can cause detrimental effects on all living things for many miles around. As a result of the 1997-98 fires, which covered a large proportion of South-east Asia, the haze was so thick that crops failed to grow and hundreds of people died from respiratory problems. Page *et al.* (2002) discovered the full extent of the damage. Using satellite images over a 2.5 million-hectare study area in Central Kalimantan, they calculated 32% (91.5% which was peatland) of the area had burned as a direct result of the 1997-98 El-Nino fires. They took burn-depth measurements of the peat and estimated that 0.19-0.23 gigatonnes (Gt) of carbon was released by means of peat combustion. An extrapolation of those data gives an estimation that between 0.81 and 2.57 Gt of carbon was released in 1997, as a consequence of burning peatlands; the equivalent to 13-40% of the average global carbon emissions from fossil fuels in one year (Page *et al.* 2002).

Millions of dollars have been spent trying to identify the origins of, and provide solutions for, these fires. One of the major problems identified was 'controlled' fires being lit on small plantation farms and, to a larger extent, by government organisations in order to clear land for agriculture (Page *et al.* 2002). The El-Nino weather phenomenon occurs every five-to-ten years and can extend the dry season for up to three months, causing critical drought conditions. The Sebangau National Park is particularly prone to fire damage, as it has a history of severe logging disturbance which fuels the fires (Figure 1.9). The major cause of this was believed to be the higher occurrence of lianas and combustible plants in disturbed forest as a result of deforestation (Wirawan 1984; Lennertze and Pazer 1984; Tagawa *et al.* 1988). Peat fires can sometimes deceivingly appear to be extinguished, but this is often not the case, as fires will continue to burn underground, destroying soil and nutritious matter that may take thousands of years to replace (Yeager 1999).

Figure 1.9 Satellite image of the Sebangau. Note the large white patches are due to fire damage and the logging canals and skids can clearly be seen all over the forest

1.4 Locomotion Techniques and Functional Anatomy

1.4.1 Brachiation

Possibly the most conspicuous part of gibbon behaviour is the way they move through the canopy. They have adopted distinct behavioural characteristics enabling them to travel at high speeds through the forest which, ultimately, allows them to exploit scattered food sources and defend exclusive rights to a territory. They are highly-specialised brachiators; hand and wrist morphology, elongated fore-limb proportions and specific body-muscle structure enable them to travel through the canopy at substantial speeds (Usherwood *et al.* 2003).

True brachiation is unique to the small apes (Hylobatidae). Some New World monkeys (*Ateles, Lagothrix, Alouatta*) have adapted a form of brachiation, using their prehensile tails as a fifth limb in locomotion (Andrew and Groves 1976; Mittermeier 1978). Orang-utans (*Pongo pymaeus*) and chimpanzees (*Pan troglodytes* and *Pan paniscus*) do adopt a similar suspended feeding posture. They will occasionally combine their travel with fore-limb suspensory bouts, but most of their suspended postures are adopted whilst feeding, although normally two limbs are used for support instead of one (Hollihn 1984). Gibbons will use two limbs instead of one if hanging in suspensory position for a long period of time. This enables them to keep balance and lead directly into locomotion (Carpenter 1976).

1.4.2 Anatomical features

Gibbons have the advantage of particularly long fore-limbs; an adaptation which has resulted from this specialised form of movement and the ability to hang bimanually over extended periods of time. It has been widely documented that the small apes spend more time in bimanual suspensory postures than any other primate (Chivers 1973; Fleagle 1976a; Mittermeier 1978). They will hang from substrates using their fore-limbs as their principal or only means of support. Resting, feeding, travelling and even copulation will take place in this suspended position. Extended fore-limbs are important in a number of ways; use during travel enables an increased arm-stride length, use in foraging enables them to climb further than the average small-bodied primate, and use during feeding enables them to exploit otherwise unreachable food sources in the terminal branches (Hollihn 1984). In order for this specialised locomotor adaptation to be successful, it needs to allow for variation and adaptability. To avoid distortion of the trunk during brachiation, the rib-cage is extremely solid, with the lower spine being short and somewhat inflexible. Gibbons, asleep or awake will instinctively grip over-head supports to steady themselves and be ready at any point to commence movement (Carpenter 1976). Brachiation through dense forest canopies involves extensive manoeuvrability and injury can cause severe locomotor modifications, such as one-armed brachiation (Gibbons and Lockwood 1982).

The gibbon hand is long and slender, with the four fingers acting as specialised hooks during brachiation (Van Horn 1972). The thumb is kept out of the way during brachiation by folding it into a deep cleft (Straus 1942). The thumbs of *Colobus* and *Ateles* have either been lost completely or reduced somewhat over the generations, but in *Hylobates* they have evolved and modified for a precision grip for picking small fruit, through specialised anatomical complexes involving the formation of bones, joints and muscles to become one of the longest primate thumbs relative to body size (Schultz 1930).

1.4.3 Evolutionary advantages of brachiation

Brachiation can be defined as the bimanual sequence of rhythmic movement along over-head structures over a distance of several metres without the aid of the hind-limbs or the use of other forms of locomotion, as demonstrated in Figure 1.10 (Napier and Napier 1967; Baldwin and Teleki 1976). There is major rotation of the wrist, elbow and shoulder joints (Carpenter 1976), with the most essential requirements of all being adequate muscle strength and a sufficient blood supply to the extended fore-limbs (Preuschoft and Demes 1984). A brachiating gibbon advances forward, not just by means of merely exchanging hand-holds, but by achieving momentum which propels the body through the air; a term called ricochetal brachiation (Hollihn 1984). The swing length will intensify with speed and ultimately progress to a 'glide' period when the gibbon has no contact with the supports (Carpenter 1976).

Suspensory locomotion is a 'full body pattern of locomotion', including full use of not only the arms but the hands, shoulders, head, and trunk. The sensory systems; balance, vision, touch, proprioception, the peripheral and central neural systems are all involved, thus implying that there are fundamental genetically-determined behavioural and structural components, that create the bimanual locomotion in gibbons. Just as bipedalism in humans gave us the freedom to make use of our hands, bimanual locomotion in gibbons has given them the opportunity to exploit other anatomical and behaviour adaptations. Walking upright has enabled the use of hands and arms as 'auxiliary balancing mechanisms' and also free to carry food. Their erect posture improves their vision and hearing (thus enhancing perception), including movement and distance perception which are fundamentally important for survival in dense tropical forests where falls can be fatal (Carpenter 1976).

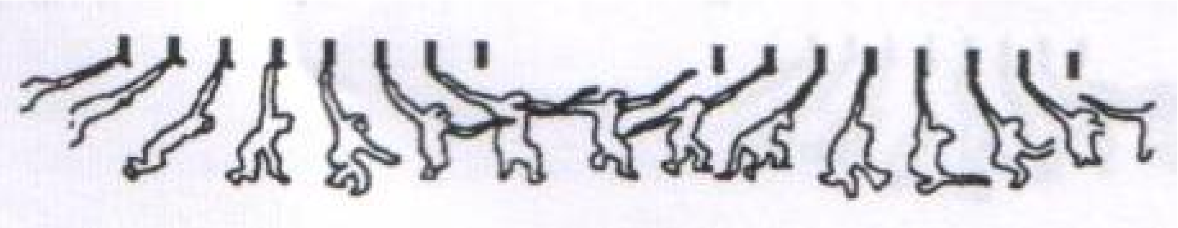


Figure 1.10 Typical brachiation cycle in a gibbon (after Usherwood *et al.* 2003)

Bimanual suspensory behaviour has fundamentally created the style and order of many different types of gibbon behaviour. It has set the style in which females carry their infants (most other non-human primates will carry infants on their backs, but gibbons always carry infants ventrally), play activities, copulation and fighting (Carpenter 1976). As gibbons are unique in their suspensory behaviours, it has been proposed that there must have been selective pressures for bimanual progression to evolve in these species.

It has been hypothesised that food gathering was a key role in the development of positional behaviours (Grand 1972; Chivers 1974; Andrews and Groves 1976). Whilst travelling, gibbons will brachiate more than whilst foraging (climbing being the dominant locomotor mode whilst foraging), but bimanual suspension is the commonest feeding position (Fleagle 1976a). This correlates with the fact that all primates spend most of their time feeding rather than travelling, thus spending more time in bimanual suspension rather than bimanual locomotion (Hollihn 1984). The advantages of adopting a suspensory posture for feeding are clear; there are far less restrictions to the food it is able to reach, thus greatly increasing its availability (Andrews and Groves 1976; Mittermeier and Fleagle 1976). The smaller the support, the greater the availability of food as the increased flexibility allows for even less restrictions (Hollihn 1984). This is a trait almost exclusively useful to gibbons; smaller primates are incapable of such suspensory behaviour and large primates are simply too large to exploit food sources in the terminal branches, for fear of being too heavy (Grand 1972).

Another theory for the selective advantage of bimanualism is predator avoidance. Moving bimanually is a much less eye-catching mode of locomotion than quadrupedal jumping, and is also a lot quieter (Grand 1972). It was observed by Tilson (1977) in his study with Mentawai simakobu monkeys *(Nasalis concolor*), that travel over long distances was uncommon, thus reducing obvious branch sway. There is also much more cover provided in the leafy foliage of the terminal branches, which may be another strategy for avoiding predators (Preuschoft and Demes 1984).

1.4.4 Perceptual motor skills

Gibbons are well known for their ability to move at great speeds through the canopy. The speed of their complex string of movements requires superior perceptual motor skills. The hypothesis of a ‘learned brain map’ has been suggested by Carpenter (1976). This ‘map’ will be a record of fruiting tree locations and travel routes the gibbon has taken and will function with instant assessment of the area to direct the individual on which pathway to take. As gibbons are constantly taking risks with airborne activities, the recorded report by Schultz (1969) of one third of all specimens having skeletal fractures, was not entirely unexpected. Many factors support the perceptual motor skill theory, the most fundamental being the speed of uninterrupted travel, the accuracy of the countless corrective acts and the limited time required for making choices between alternative travel routes. As gibbons also have relatively larger brains than folivores, their superior motor skills and higher speeds of movement can be accounted for. Day-range length and home-range size are positively related to group size and are greater in frugivores than in folivores (Clutton Brock and Harvey 1977). The amount of irregular and uneven supports present in the canopy does not respond to external forces as predictably as would a stable support (such as the ground), thus making it harder to predict reliable travel routes (Preuschoft and Demes 1984). Another strong point supporting this theory is the difference in behaviour of gibbons moving over familiar supports compared to unfamiliar supports (Carpenter 1976).

1.4.5 Evolutionary divergence

Anthropologists have illustrated brachiation as an important phase in the evolutionary development of bipedalism in humans (Napier 1963; Napier and Napier 1967; Fleagle 1981). It is widely known that humans, the great apes and the small apes share a common ancestor (Andrews and Groves 1976; Temerin and Cant 1983). Where and what caused that ancestry to diverge has been under debate for many years. Ripley (1979) stated that bimanual suspension in apes developed as a solution to reach food in the terminal branches of monolayered trees. This theory was contested by Andrews (1981) who stated unique ape locomotor behaviour like knuckle-walking, truncal erectness, forelimb dominated climbing and bimanual suspension had evolved in response to competition from Old World monkeys. Climbing is the only one of these behaviours that is unique in linking the hominoids; African apes primarily knuckle-walk, orang-utans are arboreal quadrupeds and gibbons exhibit bimanual suspension, but all climb, which is said to be the biomechanical link between brachiation and bipedalism (Fleagle *et al.* 1981). Apes were set aside from Old World monkeys as they evolved specialised post-cranial features that developed and increased abilities for suspension and propulsion by the fore-limbs (Temerin and Cant 1983).

The ultimate reason for divergence was created by different evolutionary responses to the same thing - decreasing fruit availability (Temerin and Cant 1983). This was caused by either drastic climatic change or simply high levels of competition from other frugivorous species. If animals are to sustain equivalent levels of fruit intake, they must be capable of travelling reasonably far distances in short periods of time. Attributes that accelerate the time spent travelling and foraging will be selected for naturally. These are features that ultimately lead to reduced energy costs. Monkeys and apes both have different strategies when it comes to energy expenditure. When exploiting resources in the same environment, monkeys tend to consume lower-quality food, but travel less in order to find it, whereas apes can visit more, higher-quality, food patches in less time (Temerin and Cant 1983). Ripe fruit is usually higher in nutritional quality than unripe fruit and leaves (Hamilton *et al.* 1978). Energy rates have a lower turn-over rate in larger mammals (Kleiber 1975), thus meaning they can go for longer between meals, satisfy their appetites at lower rates and exploit a widely-dispersed range of food sources.

1.4.6 Energy expenditure

There are many advantages of brachiation. One of which is thought to be its effectiveness in reducing energy expenditure. Preuschoft and Demes (1984) found that, in terminal-branch environments, suspended postures expend far less energy than any other postures. Brachiation, as a preferred form of locomotion, is ultimately energy conserving, because of the alternating conversion of kinetic energy into potential energy, and *vice versa*. Elongated fore-limbs aid energy conservation through brachiation, as the gibbon must exert less effort than an animal of a smaller body size to achieve the same pace (Preuschoft and Demes 1984). Usherwood and Bertram (2003) also support this hypothesis and state the swing phase of brachiation is unlikely to be the cause of substantial energy loss.

Energy expenditure is important in terms of, for example, reproductive success and lactation in females. Thus, it is of significance to understand the adaptive aspects of locomotion in relation to energy expended in travel. Using brachiation as the main form of locomotion increases the availability of supports and assumes the routes of travel are reduced in distance, and thus energy loss. Directness of travel, and the ability to travel quickly to dispersed, high-quality food sources, are the keys to reducing energy output (Cant 1986).

Fifty percent of all travelling in siamang is composed of suspensory locomotion (Fleagle 1976a), with 80% recorded for *H. lar* by Andrew and Groves (1976), 48-57% recorded for *H. agilis* by Cannon and Leighton (1994), and 66% recorded in this study. It may seem to be less costly energetically to brachiate than travel by any other form of locomotion, but, in *Ateles,* 20-30% more energy was expended on brachiation than on bipedal or quadrupedal walking (Parsons and Taylor 1977). This possibly also stands true for gibbons. The high frequency of use of a locomotor behaviour does not necessarily mean it is the most energy-efficient mode of travel. For instance, humans exclusively walk on two legs and need double the amount of energy required for this than a mammal of similar size needs for walking on four legs (Taylor *et al.* 1970). The capacity to lose energy from a mechanical system, such as bimanual suspension, is an unexpected factor in locomotion. Landing after a sequence of ricochetal brachiation can bring the gibbon to a sudden halt, creating a net energy loss due to negative, counter-active work in both the legs and the arms. It thus makes sense for a gibbon to travel longer distances in brachiation sequences than it does to stop and start.

Fleagle (1974) has another take on the dynamics of brachiation. He reported three fundamental ways in which a brachiating siamang can minimise energy loss: (1) by maximising the change in kinetic energy on the downswing, (2) by minimising the loss of kinetic energy on the upswing and (3) by minimising any lateral components in its momentum. An investigation of the siamang's posture during brachiation showed postural alterations that maximise efficiency in all three ways. The kinetic energy gained from the downswing is ultimately changed to potential energy and consumed again for the upswing by means of correctly timing the redistribution of body mass. After these proposals, Fleagle (1974) then hypothesised siamang could potentially acquire a net momentum from each swing, thus giving evidence into why *H. lar, agilis* and *albibarbis* are spending well over half their travel time brachiating rather than any other form of locomotion – because it is less energetically costly. Although brachiation is no doubt energetically costly in some form, it has been described by Fleagle (1974) that it is only by way of the rotation of the trunk that energy is expended.

In a study by Thorpe *et al.* (2007) orang-utan (*Pongo abelii*) energy costs were studied. It was discovered that orang-utans were using substrate compliance to decrease the energetic costs of locomotion. They do this by tree-swaying (bridging gaps between trees by shifting their weight); a locomotor behaviour which gibbons rarely exhibit (pers. comm.). This behaviour was discovered to be less than half as energetically costly as jumping or coming to the ground to cross the gap. This is the first study of its kind to assess the energetic differences between gap-crossing techniques in orang-utans. Although gibbons do not characteristically display this mode of locomotion, it highlights the different energetic costs involved in each type of locomotion.

Gaps in the forest are a significant aspect involved with increased energy expenditure. It was found by Engstrom (2000) that an increased presence of gaps was related to a reduction of orang-utan density in disturbed forest. She proposed that this was due to a higher predation risk, as the nests were built at lower heights in disturbed forest than in primary forest. Furthermore, an increase in gaps also increased the energy expenditure of orang-utans, as they were compelled to travel further to reach food sources (Engstrom 2000; Rao and van Schaik 1997). These consequences would also apply to gibbons. Although gibbons are extremely versatile when it comes to moving on the ground (their elongated fore-limbs having not limited their terrestrial abilities (Vereecke *et al.* 2006)), this presents many problems for their species. Disease transmission, susceptibility to hunters and increased predation risks are but a few of these potential risks.

1.5 Previous studies

Previously, a model called the Perceived Continuity Index (PCI) has been used to study the ecology of locomotion in agile gibbons (*Hylobates agilis*) and long-tailed macaques (*Macaca fascicularis*) (Cannon and Leighton 1994). In this study, the selections of canopy strata most preferred for travel were compared for the two species. It was concluded that locomotor behaviours and approaches to selecting the most effective route of travel are affected by forest type and the frequency of gaps present there.

So far, Cannon and Leighton (1994) are the first researchers to use PCI. The research was carried out in Gunung Palung National Park, West Kalimantan, Indonesia, where the topography is mountainous and composed of many sub-types of pristine rain-forest, from freshwater swamp to sub-montane forest (Whitmore 1984). The 15km^2 study area used is located at an elevation range of 20m to 960m a.s.l. (Cannon and Leighton 1994).

Many studies have been carried out on energy expenditure in primates (Taylor *et al.* 1970; Tucker 1970; Cant 1986; Crompton 1993; Rao and van Schaik 1997). One of the most relevant to this study being Thorpe *et al.* (2007) whose study on Sumatran orang-utans was the first to show that compliance of arboreal substrates is actually able to reduce the energy expended when crossing gaps and that tree-sway techniques were less than half as costly as either jumping or coming to the ground to cross the gap. Fleagle's (1974) study on the dynamics of a brachiating siamang and the energy transfer involved in brachiation also was vital in the analyses of these results. Many papers gave comparisons and insights into structural preference for many primate species including; siamang and lar gibbons (Fleagle 1976a,b), three lemur species (Dagosto and Yamashita 1998), red Colobus monkeys (Clutton-Broken 1993), Japanese macaques (Chatani 2003), cercopithecid monkeys (McGraw 1996) and two species of spider monkey (Mittermeier 1978). It was also important to look for differences between body size and to assess the impact this was having on the gibbon's locomotion. A few key papers, using a range of species, were important in assessing this concept; Remis (1995), Pontzer and Wrangham (2004), Doran (1993) and Sugardjito and van Hooff (1986).

1.6 Main aims

I will advance knowledge of gibbon locomotion and travel techniques in disturbed peat-swamp forest. Peat swamps are very important gibbon habitats and this will be the first study of its kind in this habitat type. Furthermore, only by describing the canopy and disturbance levels in detail can comparisons be made between different study sites at different times (Cannon and Leighton 1994). It will be interesting to see if the two studies can be compared, as Cannon and Leighton (1994) produced a short, data-limited study, whereas this study is longer with a larger sample size. The National Park, where the study site is located has been confirmed (through on-going density surveys using song quadrangulation) to hold about 30,000 individuals, and is believed to be one of the largest populations of Bornean agile gibbons left in the world (Cheyne *et al.,* in press). The locomotion data, combined with habitat data, provide essential information on how gibbon locomotion is affected by habitat disturbance and how much disturbance it takes to make a habitat unsuitable for supporting a sustainable gibbon population. The peat-swamp study area is relatively distinctive, in that it provides a very uneven canopy in which the animals travel. As this is the first study of its kind in a peat-swamp forest, interesting results have been obtained.

Some of the major questions to be addressed are as follows;

1) Are gibbons actively selecting the canopy height and forest type in which they travel?
2) Do their selections relate to different variables of forest structure?
3) How do they solve the problems of crossing gaps – and does this constrain their use of canopy strata for travel?
4) Are the gibbons using different locomotor techniques when encountering gaps?
5) How does the stability of the substrate relate to preference of use in crossing gaps?
6) Is jumping or swinging a more energy-efficient mode of travel?
7) Do body size and the presence of infants ventrally restrict travel in the canopy?

A contribution is being made to a larger on-going post-doctoral and PhD study (Dr S.M. Cheyne and M.E. Harrison) on the behaviour and feeding ecology of gibbons and orang-utans in peat-swamp forest. Knowledge and understanding of the behaviour, socio-ecology, feeding and energy intake of the sympatric apes is increased in this study. I aim to improve knowledge of how gibbons adapt to fragments of forest, where there are uneven canopy layers and gaps, thus improving understanding of how adaptable they are to disturbance and what levels of disturbance they can tolerate before their behaviour is changed permanently, i.e. they start coming to the ground to cross gaps. The frequency of coming to the ground in order to cross gaps is related to energy expenditure; travelling the least effective way possible will expend more energy than travelling in a direct line. This is hypothesised to be of particular importance to females, who will have higher energy demands due to pregnancy, lactation and infant-carrying. My results are contributing to the larger on-going study, as these data can be used to contrast energy intake from different foods against energy expenditure of different travel techniques. Gibbons are able to defend territories and ensure sufficient food supply by the use of energy-efficient travel. If the efficiency of this travel is reduced, the ability of efficient defence will also be reduced, thus having possible serious consequences.

The combined results of these studies will prove advantageous to the scientific status of the National Park and will be crucial in developing effective management plans for the protection of the forest and the reduction of gaps.

CHAPTER 2 - METHODS

2.1 Study area

2.1.1 Study site

The National Laboratory of Peat Swamp Forest (NLPSF) is a 500km^2 area of forest housing the Setia Alam Basecamp. Both are owned and operated by CIMTROP (Centre for the International Cooperation in Management of Tropical Peatland) and are situated at the northern end of the Sebangau National Park (SNP), Central Kalimantan, Indonesia (Figures 2.1 – 2.4). The Sebangau catchment ranges from pristine to disturbed peat-swamp forest and covers an area of 6000km^2 of the 22,000km^2 of tropical peat swamp found in this region. The 4km^2 grid of transects (cut for gibbon and orang-utan follows), in which the research was carried out, contains seven habituated gibbon groups that inhabit areas of varying disturbance (caused by logging, natural gaps, gaps created by bat hunters, fire and disused logging canals). The study site was previously a logging concession from 1966-96. Almost as soon as the logging concession expired, illegal loggers moved in (Husson *et al.* submitted), but thanks to the efforts of the CIMTROP patrol team, illegal logging has now been stopped in the NLPSF. Many gaps in the forest canopy still exist, however, as a result of this sustained disturbance.

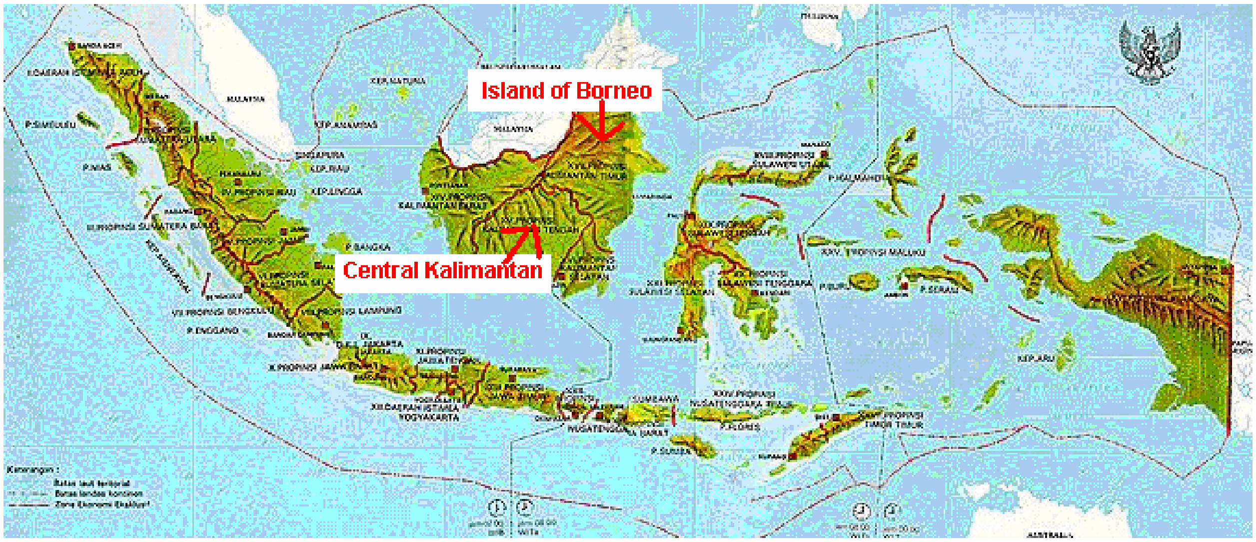


Figure 2.1 Location of Central Kalimantan within Indonesia

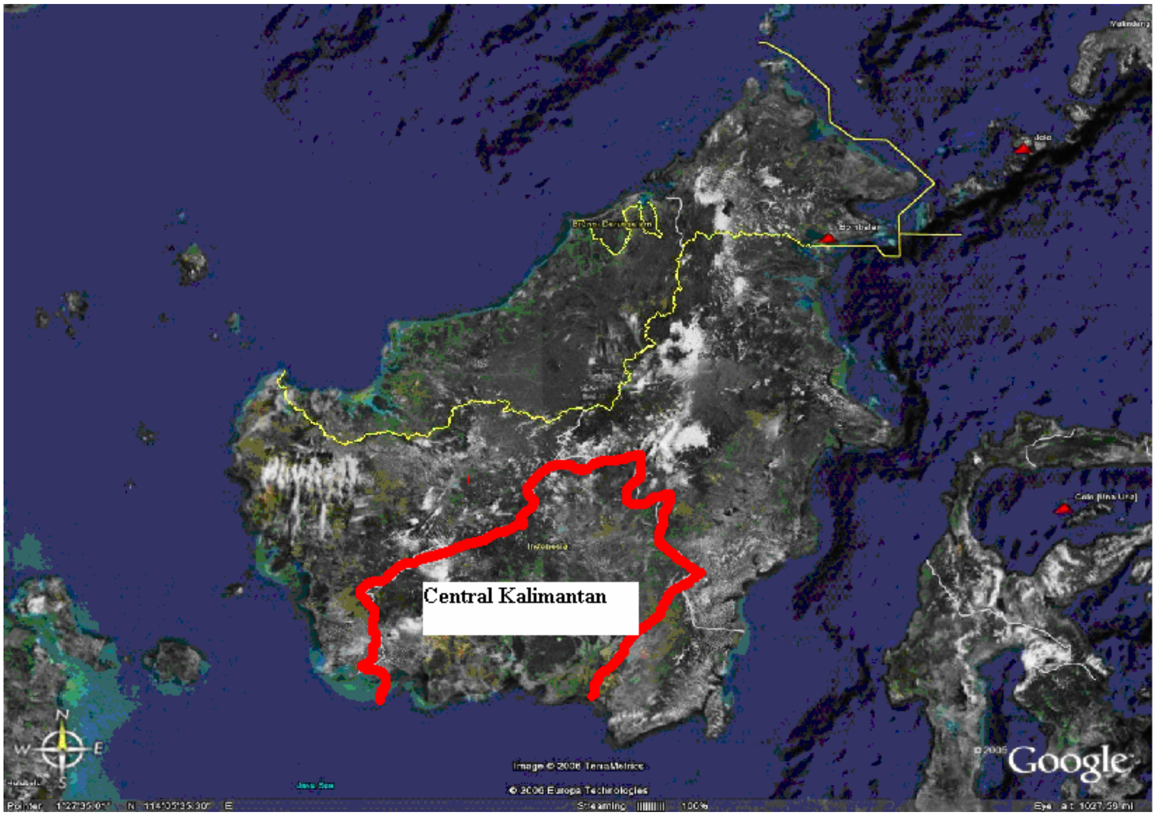


Figure 2.2 Location of Central Kalimantan within the Island of Borneo

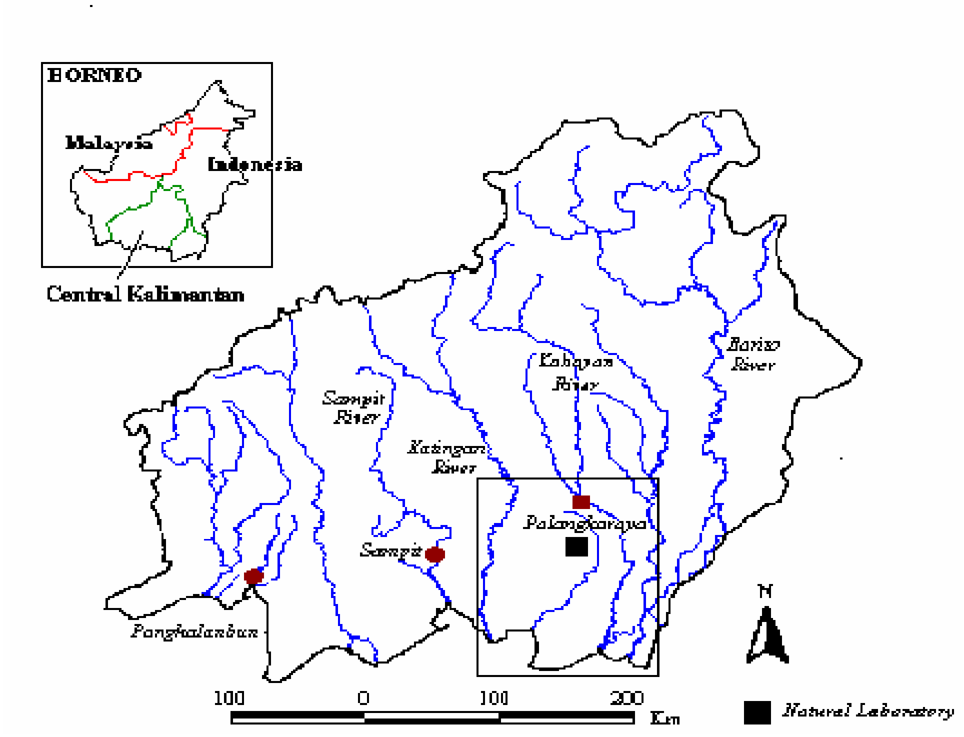


Figure 2.3 Location of Natural Laboratory within Central Kalimantan

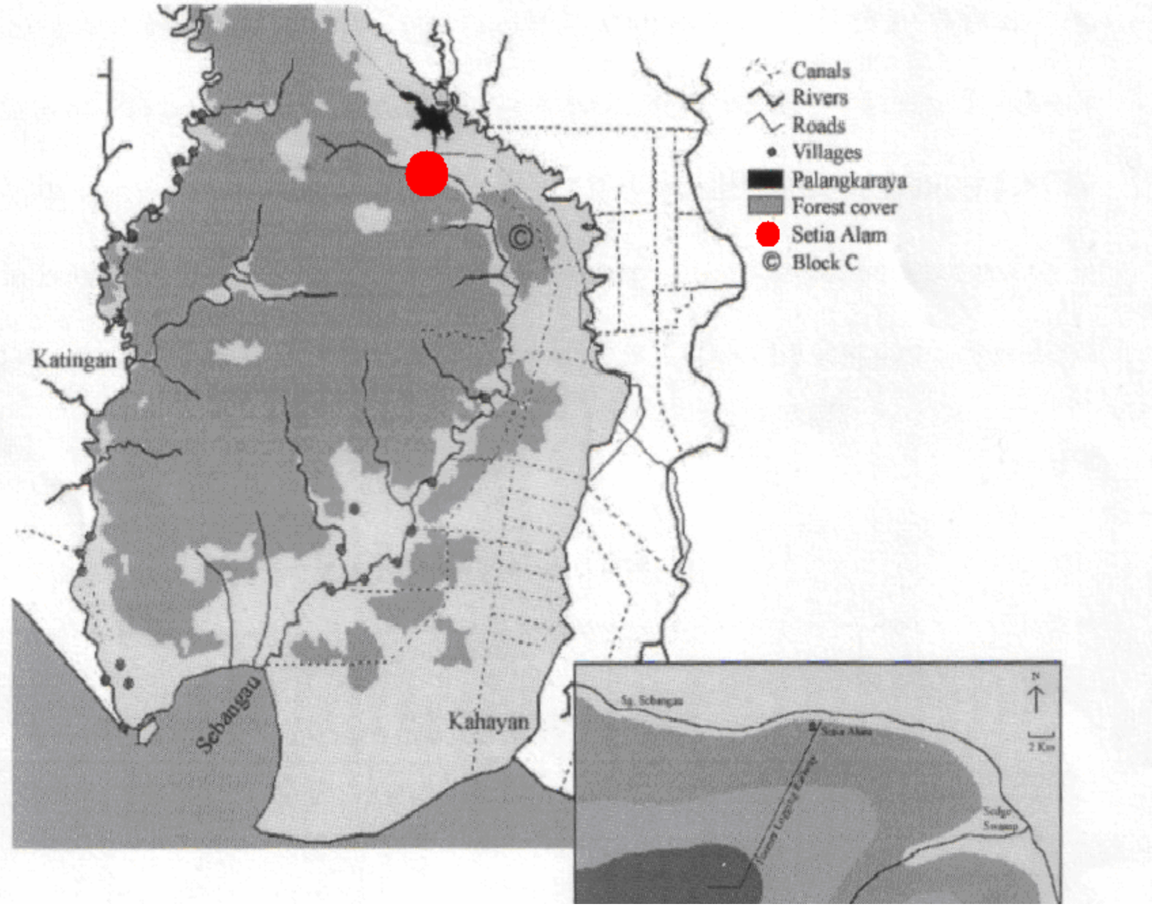


Figure 2.4 Location of Sebangau River and Setia Alam Basecamp

2.1.2 History of study site

Peat-swamp forests constitute a broad and biologically-significant ecosystem within Kalimantan, yet the forests continue to be exploited, and relatively little is known about how the habitat is affected by these disturbances or how the habitat responds to regeneration (Allinson 2003). Peat-swamp forests were formed at the end of the last glacial period as a result of rising sea-levels. The rivers deposited silt on flood plains, which gradually became less saline, as the amount of soil steadily increased with the rising sea-level. These depositions eventually formed domes of primarily-organic matter, which were not prone to flooding and could reach up to 20m in depth. As flooding was so infrequent the soil became less nutritious and more acidic (with a pH usually less than 4). In comparison to other forest ecosystems, peat-swamp forests contain less endemic species (most likely due to their recent formation) and, overall, a lower species abundance (IUCN 1991).

2.2 Study animals

2.2.1 Study groups

Below, in Table 2.1, are all the gibbons on which data were collected. A total of 1,273 instantaneous samples were recorded. Some have more data than others, but the aim was to get at least 15 jumps for each individual.

Table 2.1 Age/sex/group size data on the habituated gibbon groups used in this study. *Group C lost a member (Chivers Gibbon) on 14/02/06, due to unknown circumstances, thus lowering their group size to 4 after this date. Numbers in **bold** are gibbons with 15 or more jumps recorded

Gibbon name	**Sex**	**Age class**	**Group**	**Group size**	**No. Jumps recorded**
Ari Lasso	Male	Adult	A	4	11
Ayu	Female	Adult	A	4	6
Angus	Male	Adolescent	A	4	1
Captain Kalaweit	Male	Adult	C	5*	**347**
Coklat	Female	Adult	C	5*	**481**
Chivers Gibbon	Male	Adolescent	C	5*	**48**
Cynthia	Female	Adolescent	C	5*	**89**
Cheeka	Unknown	Infant	C	5*	0
Eno	Male	Adult	E	4	1
Endang	Female	Adult	E	4	9
Edy	Unknown	Juvenile	E	4	1
Erna	Female	Unknown	E	4	0
Bruce Lee	Male	Adult	Karate	5	**57**
Chun Li	Female	Adult	Karate	5	**99**
Zyang Ziyi	Female	Adolescent	Karate	5	10
Jet Li	Male	Juvenile	Karate	5	9
Kiki	Unknown	Infant	Karate	5	1
Manga Male	Male	Adult	Manga	4	3
Manga Female	Female	Adult	Manga	4	1
Manga sub	Male	Adolescent	Manga	4	0
Manga juvenile	Unknown	Juvenile	Manga	4	0
Ninja Boss	Male	Adult	Ninja	5	**17**

Nikmat	Female	Adult	Ninja	0	**16**
Niko	Male	Adolescent	Ninja	0	**24**
Neo	Unknown	Juvenile	Ninja	5	0
Homer	Male	Adult	Simpsons	4	3
Marge	Female	Adult	Simpsons	4	1
Bart	Male	Adolescent	Simpsons	4	0
Lisa	Female	Adolescent	Simpsons	4	0
Yoga	Male	Adult	Alone	1	**26**
Yogi	Male	Adult	Alone	1	12

The distribution of data collected for each group is shown in Figure 2.5. Group C were the most habituated group, with 74% of all observations. The female of the group was the most followed of them all, with 37% of all observations.

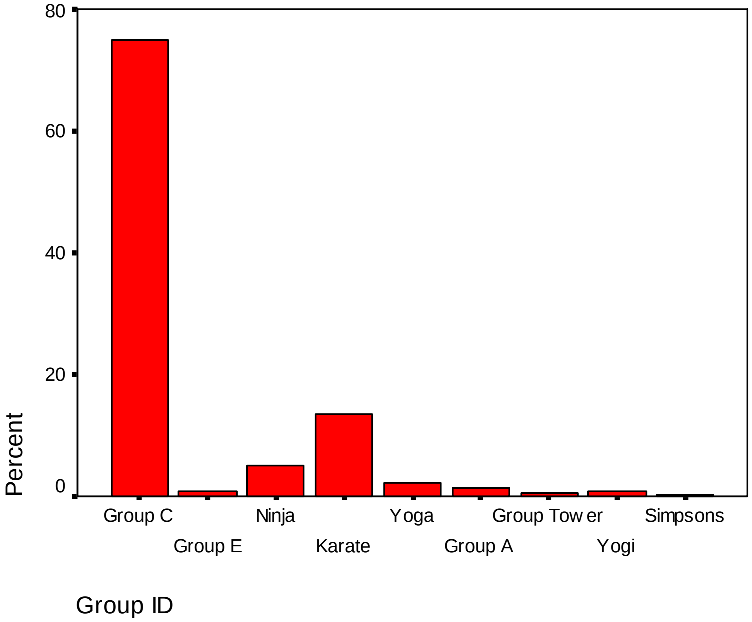


Figure 2.5 Distribution of data collection for each group

2.2.2 Territory locations

Territories were worked out by means of an on-going quadrangulation study from July to December 2005. Quadrangulation is the auditory sampling of gibbon populations by the use of three listening posts with the location of the gibbons completing the quadrangle. It is thought to be the most precise method for calculating density, particularly in areas where the population is low and gibbons are not habituated. The application of this method required previous knowledge of the average probability of an agile gibbon calling each day (Brockelman and Ali 1987; Brockelman and Srikosamatara 1993). After four days one is confident of having located all groups, although this is variable depending on the weather and season (O'Brien *et al.* 2004). Listening posts were set up 300-500m apart (see Figure 2.6), as five sets of three posts (15 in total) and each set was surveyed for 10 days each to obtain as accurate a sample as possible. The observers at each post would take compass bearings of each singing group and estimate the distance of them from the post. O'Brien *et al.* (2004) determined that calls heard more than 500m apart were to be considered separate groups, based on the rough diameter of a group's territory compared to the average distance agile gibbons move between calls. The densities in the mixed peat-swamp forest were low at 1.72 groups/km^2. The results from this study were extrapolated to the whole area, which gave an overall density of gibbons in Sebangau at about 30,000 individuals (Cheyne *et al.* 2006 in press).

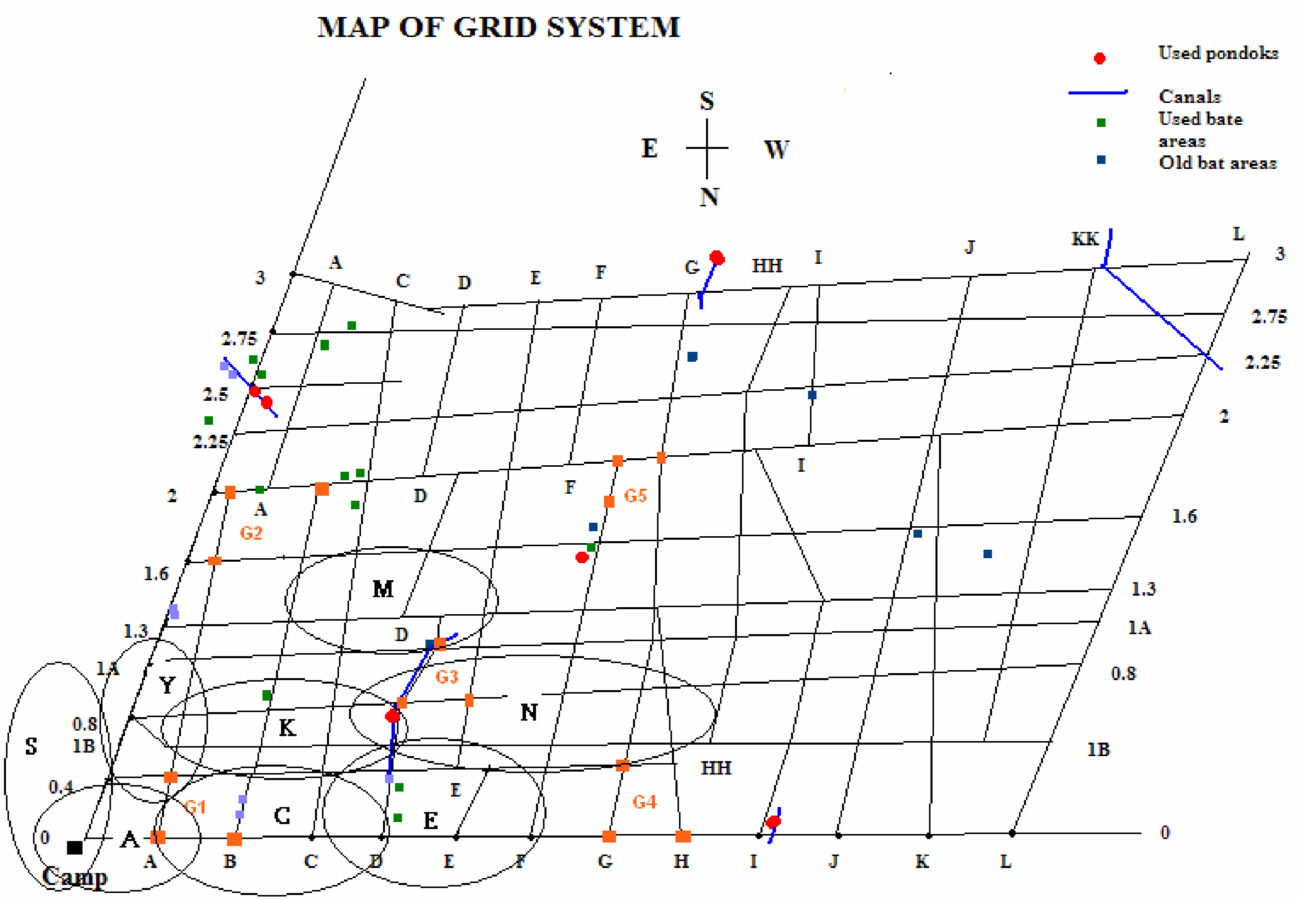


Figure 2.6 Territories of habituated groups. S= Simpsons, A= Group A, Y= Yoga, C= Group C, K= Karate, N= Ninja, M=Manga and E= Group E (from Cheyne *et al.* in press)

2.3 Methods of Behavioural Observation

2.3.1 Data Collection

Data were collected on a daily basis with the assistance of local Indonesian staff employed by CIMTROP. All staff were fully trained in following gibbons and were trained specifically in how to collect the locomotion data. Following a process of six months habituation (July-December 2005), the gibbon groups were expressing normal behaviour and could be followed from morning sleeping tree to night sleeping tree. The data sheets used to collect data contained the following categories defined in table 2.2.

Table 2.2 Definitions of data collected

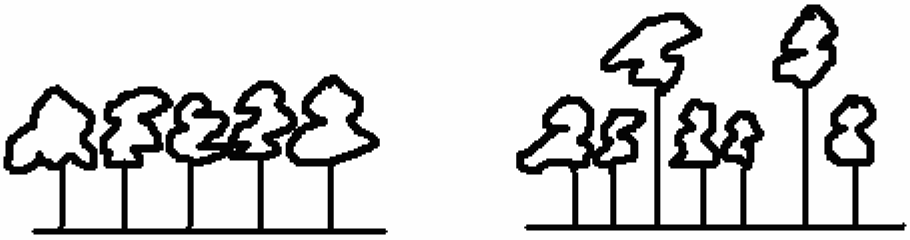
Time of jump	The time of the jump was the time (to the minute) when the animal's locomotion 'bout' began.
Gibbon ID	Gibbon identity was recorded to assess differences between age/sex classes.
Height of gibbon in first tree	Gibbon heights in trees were classified as 0-5m, 6-10m, 11-15m, 16-20m, 21-25m, 26-30m and 30m+ (trees exceeding 30m were not common in the study site). The 'first tree' was the tree the gibbon took-off from.
Height of gibbon in second tree	The 'second tree' was the tree on which the gibbon landed.
Substrate type travelled from	The substrate was also separated into four categories: tree trunk, large branch (≥ 6cm diameter at breast height - dbh), small branch (≤ 6cm dbh) and lianas. Sizes of branches were estimated by observers. This was the substrate used when taking-off.
Substrate type travelled to	This was the substrate used when landing.
Distance travelled	The distance travelled was calculated, to the nearest metre, by simple estimation of the vertical width of the gap crossed, using the length of the gibbon as a comparative guide.
Jump or swing	'Jump or swing' was observed by the take off of the animal; if the legs are used, this is classified as a jump and if the arms are used, as a swing. It was normal to see gibbons using jumping locomotion to cross large gaps in the canopy between just two trees and then using the swing (brachiation) method of locomotion to travel further

	distances between a larger number of trees (pers. obs.).
Direction of travel	The direction of travel was recorded with arrows up, down or across.
Canopy height	Height of the surrounding canopy, when combined with the canopy type, gave an indication of the habitat type used for each individual locomotion sequence.
Forest type	Forest type was categorised into four sections, continuous canopy, continuous with emergent trees, broken canopy and gaps. These categories indicated the level of disturbance encountered by the gibbon during travel.

The variables collected for all samples related to locomotor behaviour and the surrounding canopy structure. These data were presented in the forms of forest type (as shown in Figure 2.7 and defined in Table 2.3) and height of canopy (measured using a range of 5m) i.e. 6-10m, 11-15m and so on. Forest type was categorised and standardised for all observers using the diagram in Figure 2.7. Assigning the level of disturbance to four types ensured that the types were distinct, individual, and obvious for all observers to recognise. The types are defined in the table below:

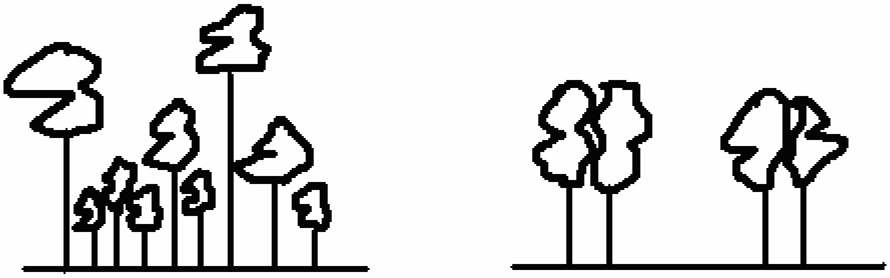
Table 2.3 Definitions of forest type

Continuous canopy	The trees all needed to be all of the same, constant height, there was not to be much undergrowth on the forest floor. This forest was very rarely found in the study area and was more common in the tall interior forest.
Continuous with emergent canopy	Not very common in the study area. For forest to fall into this type it was required to be similar to type one but have tall emergent trees and little undergrowth on the forest floor.
Broken canopy	By far the commonest found. This meant the canopy was uneven and had been through some sort of disturbance in the past. The undergrowth was normally quite thick in these areas and difficult to walk through.
Gaps	Quite common. These were areas that had been a consequence of severe disturbance, commonly due to logging skids, canals, bat towers or even large fallen trees that pull down many smaller ones with them. The undergrowth here was dependent on the age of gap (how long ago it had suffered from the disturbance). If it was relatively new there would be no or little chance for the undergrowth to grow yet, but if it had been over ten years old the undergrowth was thick and bushes and shrubs were in a greater abundance than the trees.



1. Continuous canopy

2. Continuous with emergent trees



3. Broken canopy

4. Gaps

Figure 2.7 Different types of forest

2.3.2 Travel observations

Tree height and distance estimation training was provided on a regular basis to ensure the accuracy of these data. The same definitions of forest type and tree height ranges were used in all ongoing behavioural projects at the site, thus providing a constant standard of estimation amongst all observers.

An important factor in the data collection was to ensure that a complete sequence of travel was observed. The gibbon must have been in full view from before the travel sequence began to its resting position on the landing substrate, thus enabling a full detailed description of take-off and landing substrates and heights.

The majority of observations were recorded during follows typically lasting up to 6 hours on average (although these varied greatly depending on how habituated was the group). Samples were taken opportunistically at all times of the data collection, to ensure the maximum amount of data possible was collected. An observation had to meet three criteria to be valid:

1) The focal animal must be observed before the start of locomotion (to obtain the correct take-off substrate, time of jump, direction of travel, height of take-off and jump/swing locomotion).

2) A complete sequence of travel must be observed (to obtain the correct distance estimation).

3) The end of the sequence must be observed (to obtain the correct landing substrate and the height of landing). All other data could be collected before or after (more commonly) the sequence had ended.

These criteria could possibly have been biased towards shorter sequences of travel, it being easier to record for shorter jumps, but the majority travel sequences are shorter rather than longer anyway. Many sequences were rejected if the focal animal jumped or swung into a tree and the landing substrate could not be identified. There was very little time to investigate these rejected observations, as the animals moved so quickly through the canopy.

Digital watches were used to time the start of the animals' travel sequences; data sheets and clipboards were used to record all observations and binoculars were used opportunistically at times when the animals were not moving too fast, but generally the naked eye was effective enough. Identifying individuals became progressively easier over time, as the observers became accustomed to their unique features and, on a lesser scale, their behaviour. Some were inquisitive and some appeared very shy. Two of the females carried infants ventrally, making them easy to distinguish, and the males were generally larger with fluffy white cheeks and testicular hair tufts. Group composition could be identified from the calls; the sub-adult females practised their great-calls and each sex, having a unique repertoire, made them easy to identify whilst singing.

It was decided to focus only on the two main forms of locomotion – jumping and swinging, as opposed to the seven used in Cannon and Leighton (1994). This was decided as they are the commonest locomotor modes, with gibbons brachiating (swinging) 48% and jumping 16% of the time during travel. The other locomotor modes used in Cannon and Leighton's (1994) study; stepping (14.7%), bipedal walking (12%), climbing (5.3%), scrambling (4%) and bridging (0%) were not employed enough by the study animals to justify using them in this study.

The two forms of locomotion had to be defined and a constant method of identifying each had to be employed.

Swinging (or brachiation) was defined by the suspended arm posture of the animal and the lack of propulsion from the hind limbs. True brachiation is found in gibbons, as, with each swinging movement, the arm swings under the shoulder; with the large apes, such as orang-utans, the arm would be kept overhead (Sugardjito 1982). To begin a sequence of brachiation a gibbon will often head downwards, thereby achieving as much momentum as possible. As the gibbon moves forward it becomes like a pendulum, the gibbon rotates and stretches out the free arm, grabbing the over-head superstrate. The hand is then rotated to grab the superstrate to control for lateral sway. Meanwhile, the out-stretched arm pulls the body forward, thus increasing momentum further. There is unparalleled rotation of the wrist, elbow and shoulder joints. When the first arm lets go of the superstrate and is propelled forward for the next point of contact, the cycle of brachiation is complete. This cycle is repeated until the locomotor mode changes, as shown in Figures 2.8 and 2.9 (Carpenter 1976; Fleagle 1976a).

Jumping (or leaping) was defined by the distinctive use of the legs for propulsion, whilst taking-off from a substrate. It also can have a distinct behavioural cycle of movement. The gibbon must first prepare for the jump; judge distances and correctly position the limbs. It then takes-off from the substrate, using as much propulsion as possible from the legs and extends its body mid-air to maximise momentum. Landing will involve seizing the substrate with hands and first then feet. Finally, the recovery phase, which generally merges in with the next locomotor action, as shown in Figures 2.10 and 2.11 (Carpenter 1976; Fleagle 1976a). This locomotor mode is better used when crossing gaps or large distances (as more force is involved) and is instigated from the terminal branches of one tree to another. Reported leaps in siamang have been up to 20m vertically, but rarely cover 10m horizontally (Fleagle 1976a). All measurements for swings and jumps in this study have been taken as vertical estimates.

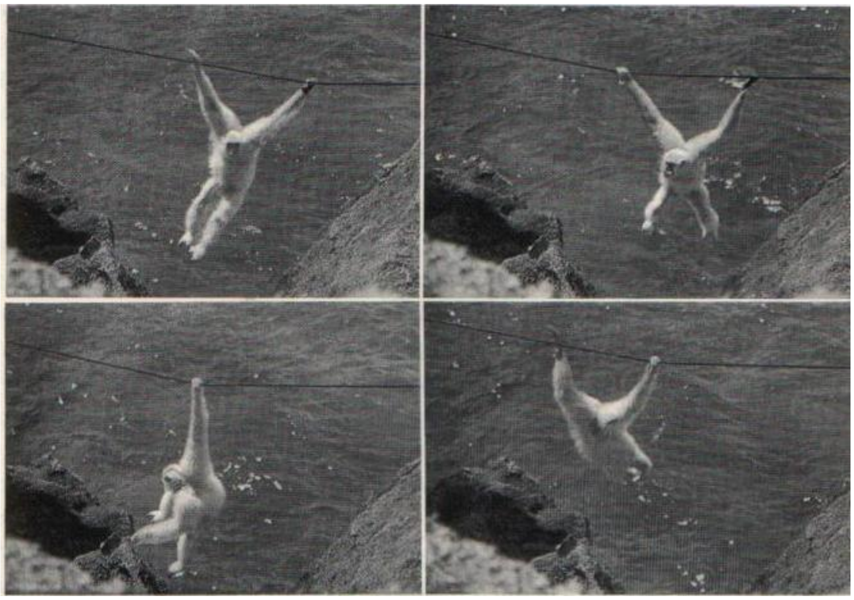


Figure 2.8 Typical brachiation cycle in a gibbon (*Hylobates lar*) (after Carpenter 1976)

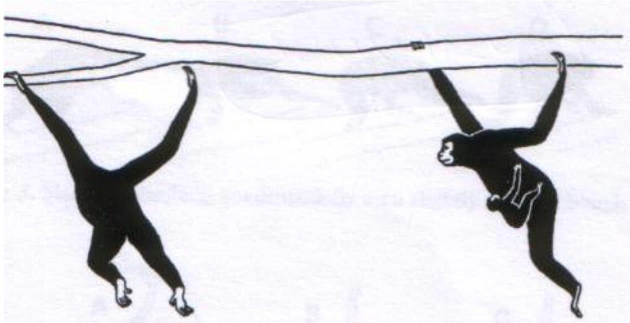


Figure 2.9 Brachiation exhibited by a siamang (after Fleagle 1976a)

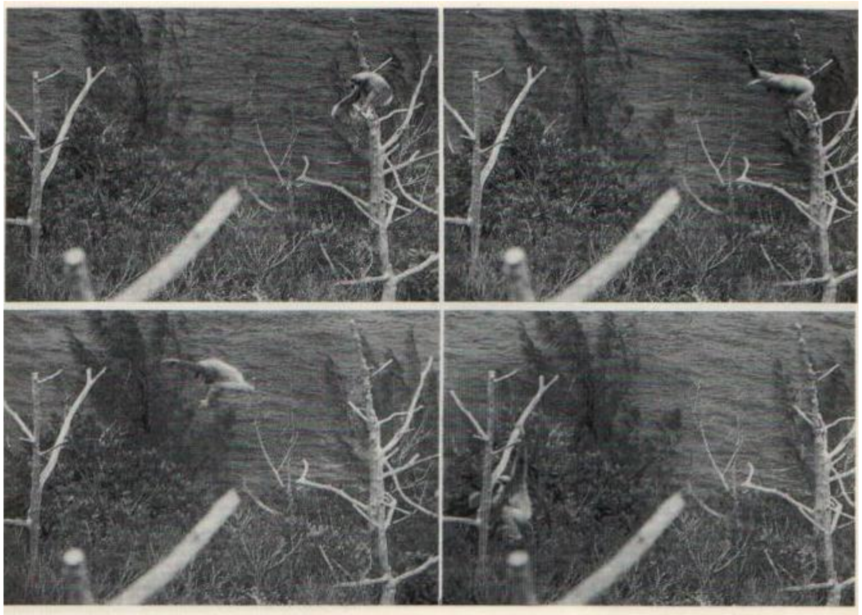


Figure 2.10 Typical jumping locomotion in a gibbon (*Hylobates lar*) (after Carpenter 1976)

Figure 2.11 Jumping behaviour exhibited by a siamang (after Fleagle 1976a)

2.4 Methods of Habitat Data Collection

2.4.1 Data Collection

Habitat data were collected in order to compare the frequency of use of habitat structure to its frequency of availability. In order to do this, four plots were set up randomly in each of the six group's territories (Group A and Yoga's territory were combined as they occupied roughly the same area). Their locations were produced using the random-number generator on a calculator and were plotted onto a map of the study site, with the only constraint being that they were not near any of the original transects used for walking, as this would distort the results and be biased towards the more disturbed areas. The plots are shown as red dots in Figure 2.12. Methods were adapted from those used in Cannon and Leighton (1994) to create a more random and varied insight into the availability of canopy structures.

Twenty-four (four/group) 50m transects were constructed within the territories of each of the six groups. Cannon and Leighton (1994) used 100m transects, but only had 2 for each habitat type. The same quantity of data (200m in total for each territory/habitat type) are analysed, but adapting to this method allows for more random variation and, thus, a broader, more accurate picture of the forest in general. At 25m intervals along each transect (3 points/transects, 72 points in total), the distance to the nearest tree >10cm dbh was measured by means of the point-centred quarter method (Mueller-Dombois and Ellenberg 1977). At 25m intervals along the transect (3 points/transect, 72 lines in total), a 20m line was laid at right angles to the transect on alternating sides. At 5m intervals along this line (5 points/line, 360 in total) the forest type and canopy height were sampled. An example of these transects can be found in Figure 2.13. The transects were always moved at least 25m away from any original tracks used for walking, so as to give a fair representation of the forest structure.

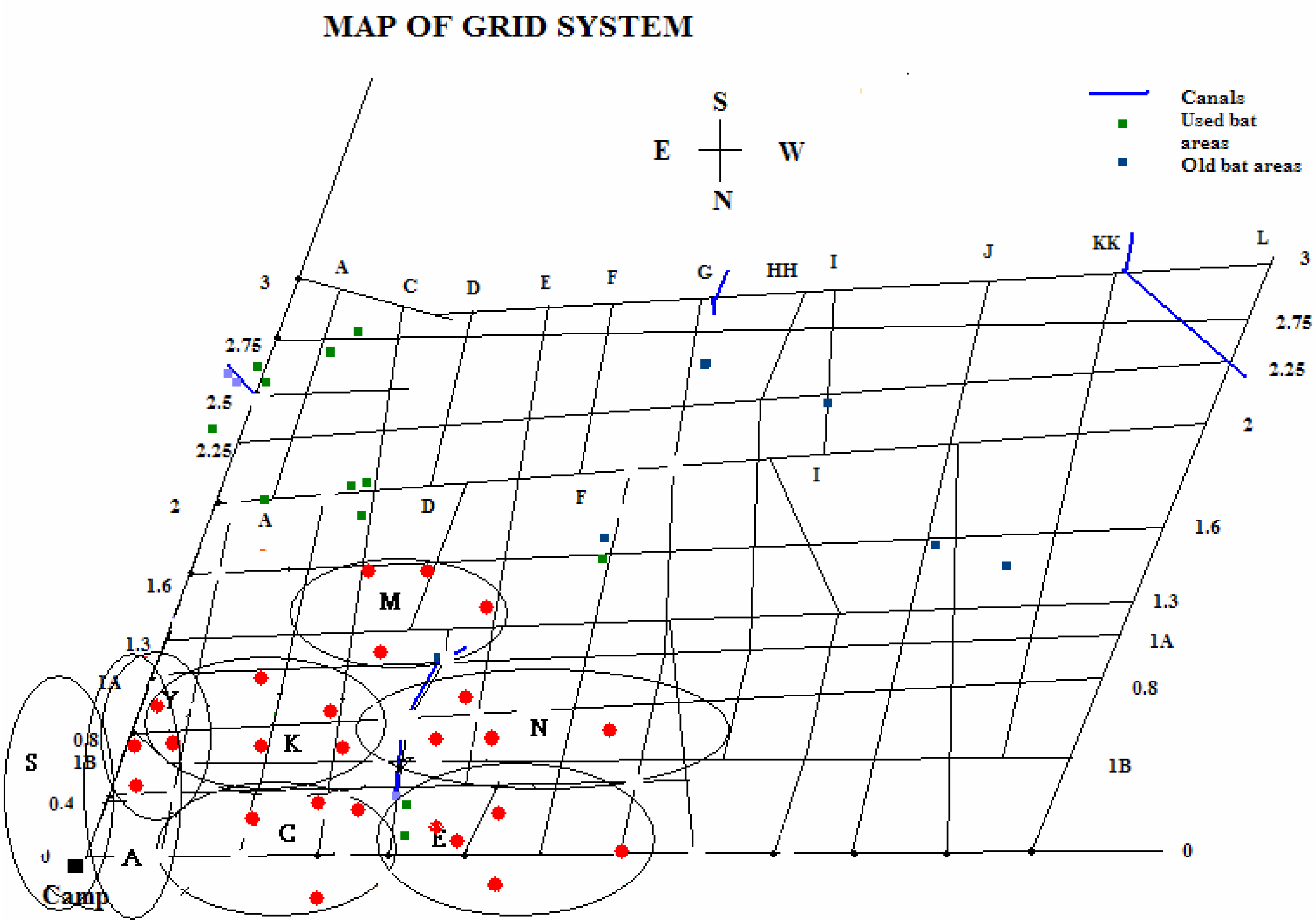


Figure 2.12 Habitat plots for each group's territory S= Simpsons, A= Group A, Y= Yoga, C= Group C, K= Karate, N= Ninja, M=Manga and E= Group E

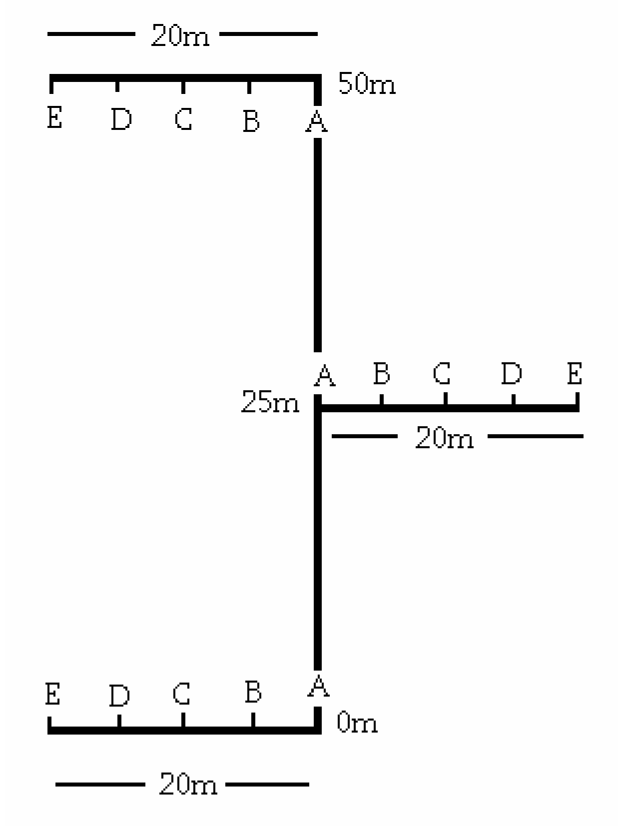


Figure 2.13 50m habitat transect used in all territories

The two variables used for the point-centred quarter method were the diameter at breast height (hereafter, dbh) size of the trees (providing they were >10cm dbh) and the distance to the nearest tree from the sample point. An example is shown in Figure 2.14. Measurements were taken at each 25m interval on the main transect (0m, 25m and 50m). This method enabled four trees to be measured for each point-centred quarter sample point, one tree in each of the sections, and its distance to the centre point. These measurements were taken with a dbh tape and measuring tape.

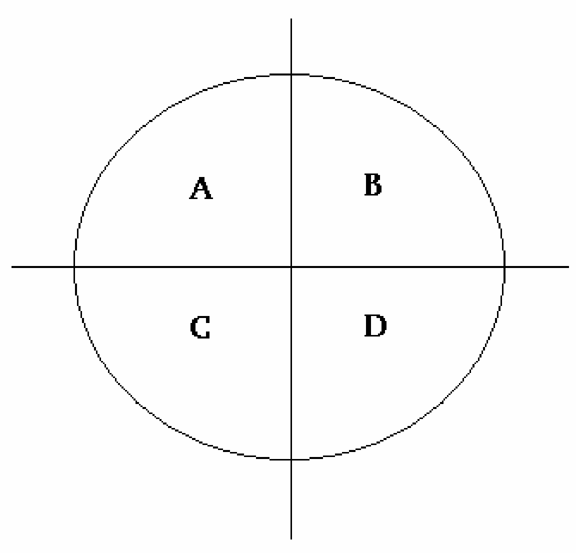


Figure 2.14 Point-centred quarter method

Measurements for the variables of forest type and canopy height were taken at each 5m interval on the 20m alternate line transects (0m, 5m, 10m, 15m and 20m) using the line-intercept method. These were kept constant with the locomotion data to enable comparative analysis between the frequency of use and the frequency of availability. Gaps were encountered throughout the territories and their frequency and size dimensions were noted at each point.

Data analysis was performed on SPSS version 11.5 and a range of statistical methods were used, including the Kruskal-Wallis chi-squared, ANOVA, Chi-squared and Tukey's *post-hoc* tests.

CHAPTER 3 – RESULTS AND DISCUSSION

3.1 Selection of canopy heights and forest type for travel

Are gibbons actively selecting the canopy height and forest type in which they travel?

Gibbons are mammals that show monogamous territoriality, using loud songs to defend an area. This is an evolutionary social strategy for minimising reproductive wastage, foraging efforts and intra-specific competition. This strategy is only suited to long-lived, highly-energetic, specialised animals and has certain drawbacks, such as evolutionary and ecological inflexibility, that leaves such species very susceptible to changes in their environment (MacKinnon and MacKinnon 1984).

It is generally assumed that gibbons will select the better forest types over the worse and higher canopies over low. It has been seen in other species, such as red colobus (*Procolobus badius*), and spider monkeys (*Ateles paniscus*), where they habitually use the upper canopy, the understorey is rarely used and they seldom come to the ground (Clutton-Brock 1973, Mittermeier 1978). As they are a highly arboreal species, this is generally the accepted notion. Cannon and Leighton (1994) conducted a study whereby they concluded that gibbon locomotor behaviour was highly affected by the presence of canopy gaps and was fundamentally based on selection of the most direct route through the canopy. During travel, gibbons tend to follow established routes through the trees, referred to as arboreal highways (Chivers 1974). This will minimise their chance of encountering gaps and also provides support for the theory that they appear to be selecting actively certain structures for travel. I explore this and consider which types of habitat the gibbons appear to prefer, by testing whether there were significant differences in the following hypotheses:

H1 *– Height of canopy between different forest types.*
H2 *– Canopy heights used by all groups.*
H3 *– Use of canopy height between different group territories.*
H4 *– Canopy height availability in all group territories.*
H5 *– Canopy height availability between different group territories.*

H6 – *Forest type used by all gibbon groups.*
H7 – *Use of forest type between different group territories.*
H8 – *Forest types available to all gibbon groups.*
H9 – *Forest types availability between different group territories.*

H1 supports that canopy heights are similar between all forest types (ANOVA=2.361, 4 d.f., P>0.05). Thus, we can assume that there is a relatively equal availability of structures of various heights in each forest type. Gaps had the only occurrence of 0-5m heights and the highest occurrence of trees of between 26 and 35m **(Figure 3.1)**, suggesting uneven structure, which is probably not favourable for travel, as the animal would be constantly ascending and descending, ultimately expending more energy than going straight across an even array of structures. This supports ***H2,*** as all groups are generally using the same canopy heights for travel and not continuously going up and down (X^2=1106.374, 6 d.f., P<0.05). They are mainly using heights between 11 and 25m, other heights are used very rarely **(Figure 3.2)**. Cannon and Leighton (1994) state that their study gibbons *(H. agilis)* prefer larger (48cm dbh), taller trees (31m) in the emergent canopy layer, which had 28% presence within the habitat, but in Sebangau the occurrence of trees in the height-class 31-35m was only 0.1%, thus forcing the gibbons to travel at lower heights due simply to lack of availability. Looking for differences between groups, ***H3*** suggests that Group E was the only significantly different group (F=5.937, 8 d.f., P<0.05), to all others apart from Manga **(Figure 3.3)**. Data for Group E and Manga were limited compared to data on other groups **(Figure 2.5)**, which may have affected the results. Assuming that they were taken out of the equation, all other groups would not be significantly different to each other, suggesting that all groups appear to be selecting roughly the same heights for travel.

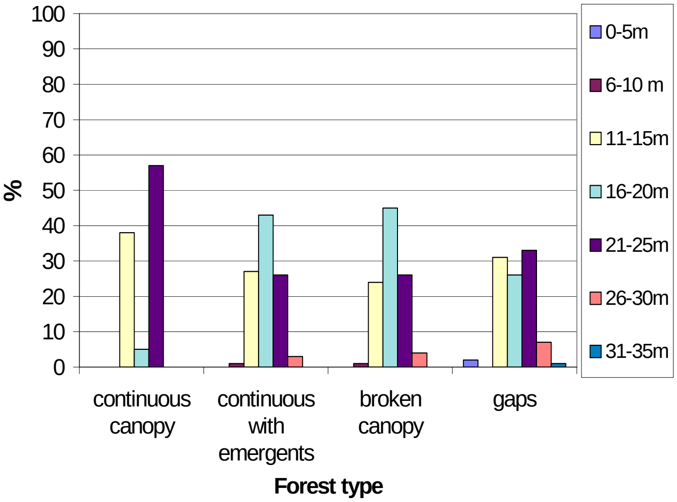


Figure 3.1 Percentage use in different height-classes in each forest type

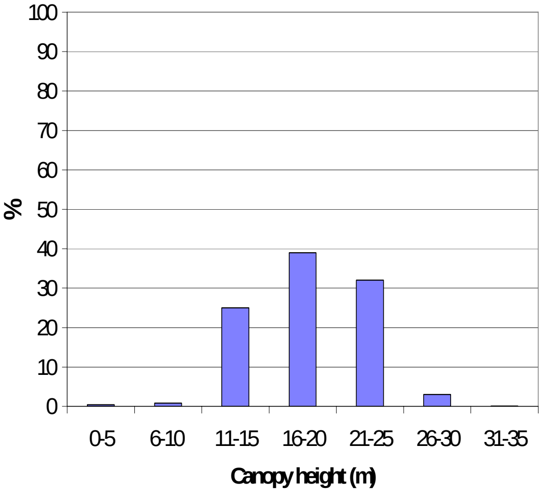


Figure 3.2 Percentage use of various canopy height-classes for all individuals over all forest types

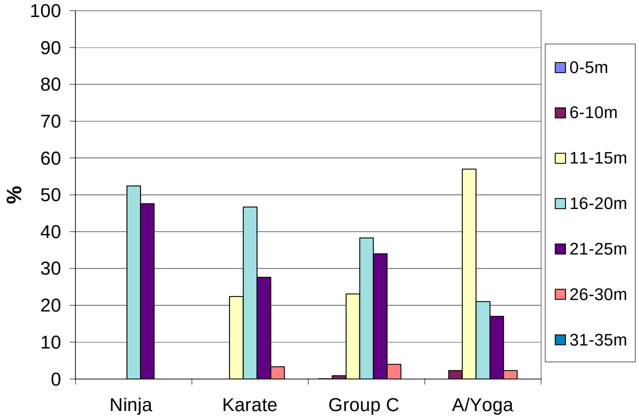


Figure 3.3 Percentage use of canopy height-classes by each group

H4 supports the significant difference between the availability of canopy heights in all group territories (X^2=25.889, 3 d.f., P<0.05). The most prevalent heights were between 11 and 25m, the other heights tested were very rarely found, suggesting that the trees often did not reach over 25m and, if they did, they were exceptional emergents **(Figure 3.4)**. This indicates the poor quality of the forest. More heights of 6-10m are available than used, suggesting an avoidance of this habitat, whereas more heights of 26-30m are used than are available, suggesting a preference for this canopy height. Looking at differences between groups **(Figure 3.5)**, ***H5*** suggests that that only Group C and A/Yoga's territories were different to the others (F=19.548, 5 d.f., P<0.05). Group C is also different in terms of forest type, but A/Yoga is not. A/Yoga's territory crosses over the railway, thus presenting the same problems as Group C – damage due to human disturbance. A small railway was constructed over 10 years ago, stretching 12km into the forest and the vegetation on either side of it has been severely damaged as a result. This would explain the difference found between these groups and all other groups, who tend to inhabit interior regions of the forest.

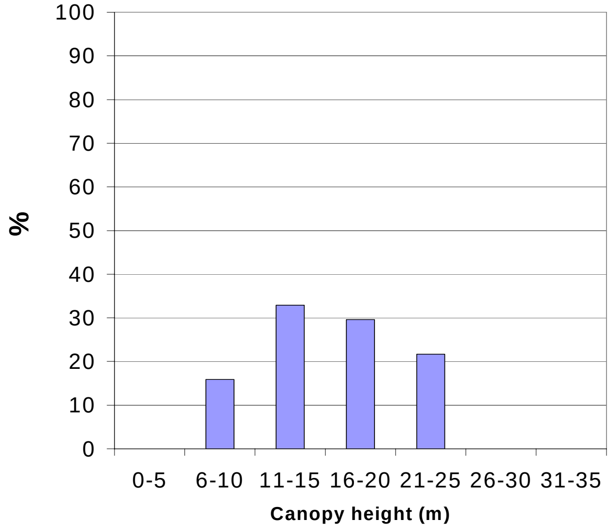


Figure 3.4 Percentage availability of canopy height-classes for all territories

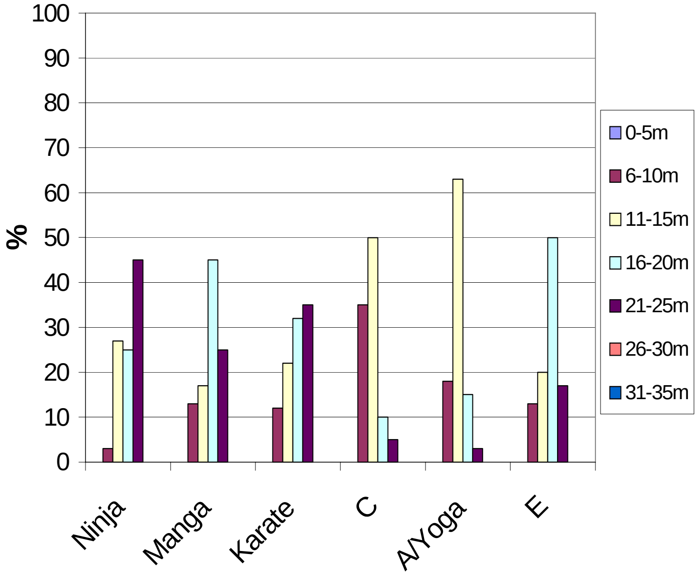


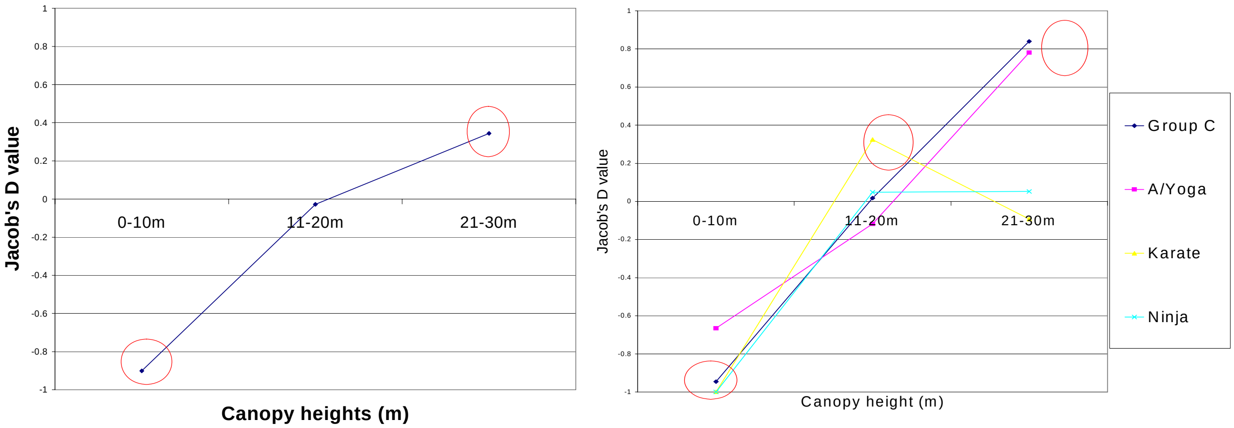
Figure 3.5 Percentage availability of canopy height-classes in all group's territories

Jacob's D Value is an index used to test for preference between different strata and has previously been used to test between food selection and abundance (Jacobs 1974). $D = (r-p)/(r+p-2rp)$

r = relative frequency and use and p= relative frequency of availability.

The Jacob's D value could only be computed for Group C, A/Yoga, Karate and Ninja as all values had to be ≥1.0 and the other groups all had at least one value of zero for one of the sample points. The observed and expected results were tested using a Chi-square test and significant results are shown in **Figures 3.6** and **3.7**. Individuals generally appeared to favour higher canopy heights over lower ones and to be actively avoiding heights of 10m and under. They neither select nor avoid mid-way heights of 11-20m, probably as they use these as stepping stones to reach higher heights. The gibbons in Cannon and Leighton (1994) also appeared to avoid the low height-classes, and strongly preferred the emergent layer (equivalent of 31-35m in this study) where 32% of travel occurred. The quality of forest obviously differs between each study, but the fundamental result remains the same, gibbons appear to be selecting higher height-classes.

Looking at each group individually **(Figure 3.7);** they all prefer higher canopy heights (21-30m), apart from Karate who show a slight avoidance of them (although this is not significant). This could be caused by the group composition, as this is the only group with a semi-dependent infant; perhaps they are travelling lower as a group to avoid predation from above. Generally, they are all following a similar pattern of canopy use, which is expected among arboreal apes. The frequency of availability of canopy heights under 20m is high, as shown in **Figure 3.4**, thus indicating that the gibbons are being forced to live in unsuitable habitats.



Figures 3.6 and 3.7 Jacob’s D Value of canopy height for all groups combined and each group individually, respectively. Positive values indicate preference whilst negative values indicate avoidance and zero values indicate neutrality. The red circles indicate significant results ($P<0.05$) in a 2x2 contingency table for that canopy height-classes

Take-off and landing heights are coherent with each other as are the heights the gibbons are selecting for travel, as shown in **Figures 3.8** and **3.9**. The canopy heights (**Figure 3.2**), show the frequency of heights of which the surrounding canopy consisted at each sample point. Surrounding canopy heights were mainly 16-20m (27%) and 21-25m (23%), whereas the heights selected for travel were lower, with the preferred height being 11-15m (44% and 43%, respectively), thus suggesting that the gibbons select the main canopy rather than the emergent layer for travel most of the time.

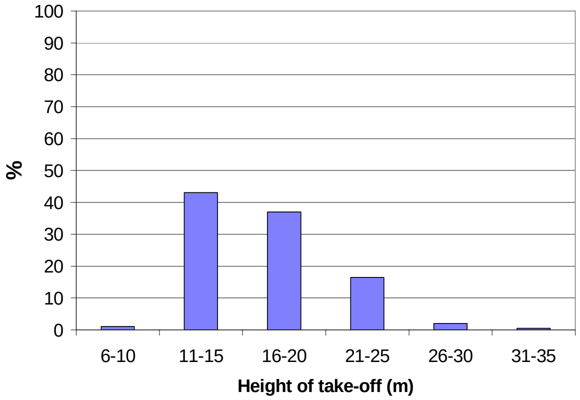


Figure 3.8 Height of take-off for all individuals in all forest types

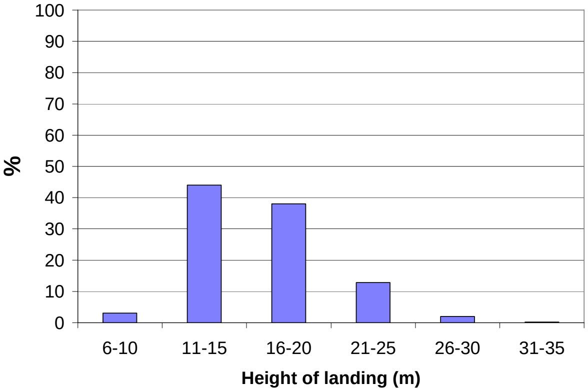


Figure 3.9 Height of landing for all individuals in all forest types

H6 supports that there is a significant difference in forest type used by all groups ($X^2=1272.139$, 4 d.f., $P<0.05$). This is unsurprising as the whole area had been subject to logging practices for more than ten years, thus proving that the area is mainly composed of disturbed habitats, or 'broken canopy' **(Figure 3.10)**. ***H7*** indicates that gibbons, as a species, will be consistent in selecting the same forest types as each other in which to travel **(Figure 3.11),** as there is no significant difference in the use of forest type between each group ($F=1.353$, 5 d.f., $P>0.05$).

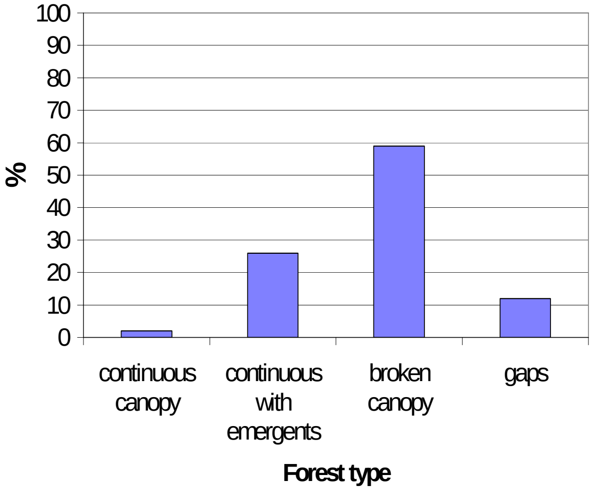


Figure 3.10 Percentage use recorded in each forest type

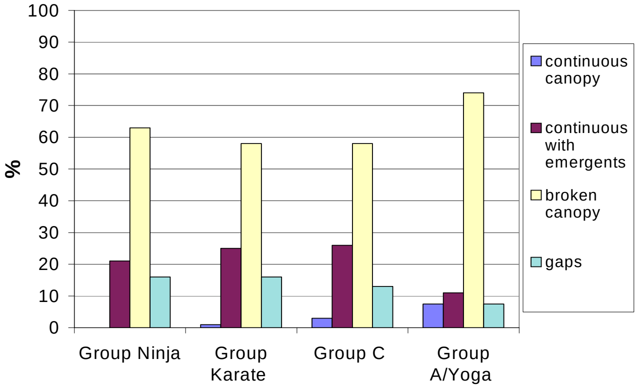


Figure 3.11 Percentage use for each group in different forest types

H8 supports that there is a significant difference in forest types available to all groups (X^2=106.650, 2 d.f., $P<0.05$). These data correlate with ***H6,*** in that they show the habitat available to the gibbons mainly consists of disturbed areas – broken canopy (58%) and gaps (25%). More gaps are available to them than they choose to use, initially suggesting they would rather avoid these areas **(Figure 3.12)**. Looking at each group individually, Group C's territory is the only one significantly different to the others (F=7.329, 5 d.f., $P<0.05$), as they inhabit an area with a higher prevalence of disturbed forest, because their home range is closest to the edge of the forest, and thus the environment is more damaged than the interior **(Figure 3.13)**.

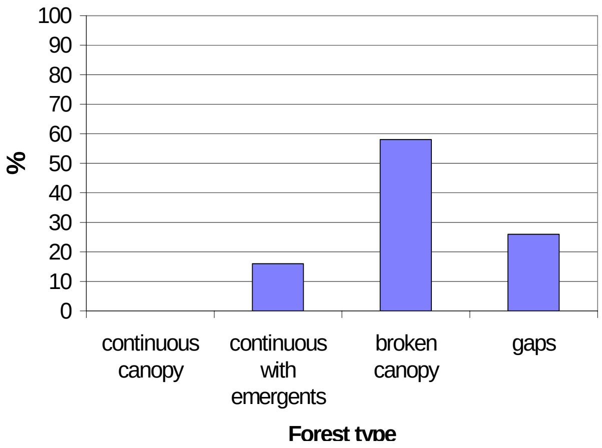


Figure 3.12 Percentage availability of each forest type over all group territories

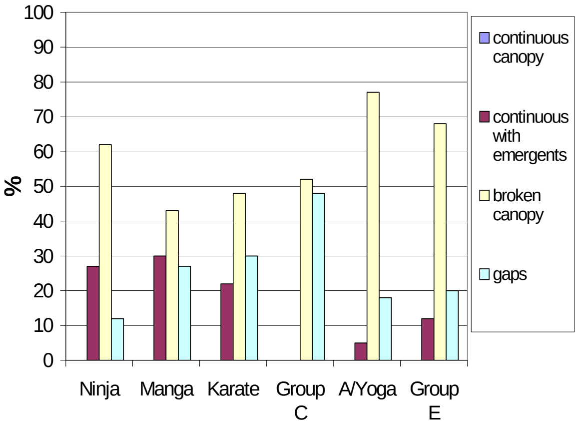


Figure 3.13 Percentage availability of each forest type in each group's territory

The Jacob's D value could only be computed if the expected values were ≥1.0, so 'continuous canopy' and continuous with emergents' were combined for analysis as the frequency of availability for 'continuous canopy' was constantly zero. The observed and expected results were tested using a Chi-square test and significant results are shown in **Figures 3.14** and **3.15**. These results show that all groups appear to avoid gaps, prefer 'continuous canopy' and 'continuous with emergents' and seem neutral to 'broken canopy'. As shown in **Figure 3.10**, the amount of time spent in 'broken canopy' far outweighs the others. This could be because they are forced into this less-ideal forest type most of the time, as they have little other choice. These data represent an accurate picture of the forest types gibbons spend their time in, and how they may be being forced into areas less preferable than they would like. The physical and emotional consequence this has caused is unknown, but it seems that the gibbons live in a far-from-ideal environment that has, and still is, deteriorating.

Looking at each group individually **(Figure 3.15),** there appears to be much variation between preferences for certain forest types. Ninja is the only group that slightly avoids the best forest type and appears to prefer gaps (although this was not significant). This may be due to the sample size being small or, perhaps, they simply have to use this canopy due to lack of choice.

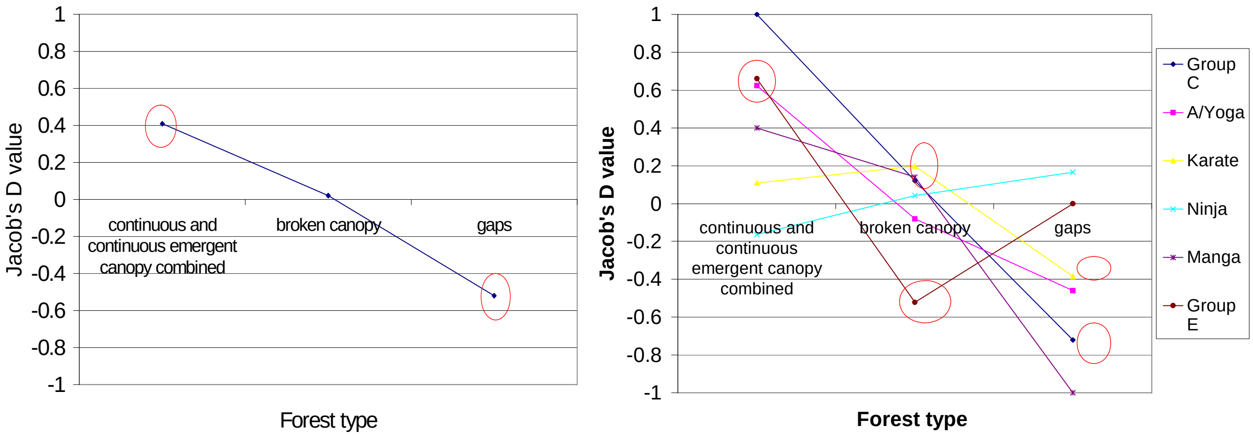


Figure 3.14 and 3.15 Jacob's D value of forest type for all groups combined and each group individually, respectively. Positive values indicate preference, negative values indicate avoidance and zero values indicate neutrality. The red circles indicate significant results ($P<0.05$) in a 2x2 contingency table for that forest type

3.1.1 Summary

In sum, the results of these hypotheses indicate that, across all forest types, the canopy heights are relatively similar ***(H1),*** 11-25m were the most commonly used ***(H2)*** and all groups (apart from Group E) travelled at roughly the same heights ***(H3)***. In correlation with ***H2,*** canopy heights of 11-25m were also more widely available to the gibbons than any other height ***(H4)*** and it was only Group C and A/Yoga's territories that were different to the others ***(H5)***. In terms of forest type, broken canopy was the most widely used ***(H6)***, and all groups travelled in the same forest types ***(H7)***. In correlation with ***H6***, broken canopy compiled a high proportion of forest types ***(H8)*** and it was only Group C's territory that was different to the others ***(H9)***. McGraw (1996) carried out work with cercopithecid monkeys and discovered that they were using a constant array of substrate type, regardless of variation in the availability of substrate types across forest types. He noted the most obvious example to be between *Colobus badius* and *C. polykomos,* who choose larger substrates regardless of canopy height or forest type, despite having the rarest availability. These results support this study as evidence for apparent active selection. Along with the Jacob's D results, these tests provide substantial support for the general hypothesis that gibbons appear to be actively selecting certain canopy heights and forest types for travel.

3.2 Different variables of forest structure

Do their selections relate to different variables of forest structure?

Variation in the size, flexibility, angle, distribution and abundance of substrates is widely regarded both to, influence and limit specific types of positional behaviour (Napier and Napier 1967; MacKinnon and MacKinnon 1978; Fleagle 1978). Larger-bodied primates will use larger, stronger substrates to support their weight, whereas smaller-bodied primates are capable of exploiting a broader selection of different-sized substrates and are not restricted by large-support availability. If larger-bodied primates are restricted by the size of substrates within a given forest type, then these individuals will demonstrate less disparity in locomotor techniques between forest types. For smaller primates, a less reliable relationship will exist between the abundance of different-sized supports and the height at which the individual spends its time, primarily because of their greater ability to use a greater array of substrates (McGraw 1996). Some authors have described rain-forests to consist of three main structural layers, the understorey, main canopy and emergent layer (Fleagle 1976a,b; Cannon and Leighton 1994). The understorey contains trees of low heights that are discontinuous horizontally and supports that are much weaker than those of the main canopy. The main canopy contains many large trees and is horizontally continuous with an arrangement of large branches and tree trunks. The emergent layer consists of large trees that surface above the main canopy and require jumping long distances or climbing to reach their large boughs (Fleagle 1976a,b). Do take-off and landing substrates have an influence on travel between different canopy heights or areas of varying forest type? This is explored by testing whether there were significant differences in the following hypotheses:

H10 *– Frequency of use of different substrates.*

H11 *– Height of take-off between different take-off substrates.*

H12 *– Height of take-off between different landing substrates.*

H13 *– Preference of take-off substrates between each forest type.*

H14 *– Preference of landing substrates between each forest type.*

H10 supports the significant difference in the use of different substrate types across all individuals ($X^2=3045.131$, 3 d.f., $P<0.05$). Small branches are more prominently used in take-off and landing, potentially to increase the crossing length by reaching the terminal branches. This is consistent with large branches being second commonest, tree trunks, and then lianas, which were used very rarely, probably due to the instability of the support **(Figure 3.16)**. In Fleagle (1976a,b), branches over 10cm dbh were the commonest used by lar gibbons (*Hylobates lar*), smaller branches of between 2 and 10cm dbh were the second commonest and anything below that was never recorded. This could be to do with differences in forest type or simply topographic between study sites.

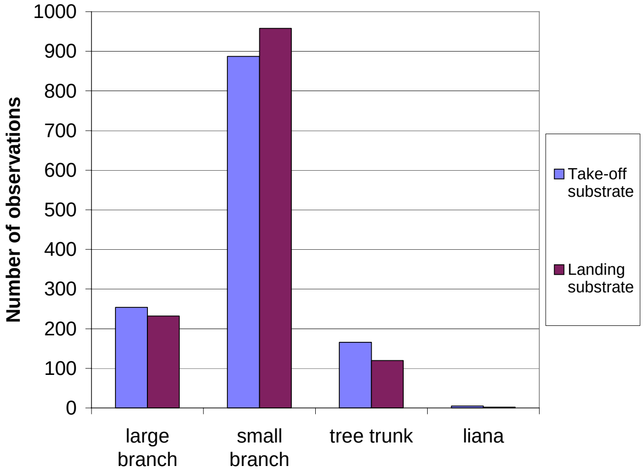


Figure 3.16 Frequency of use of different take-off and landing substrates

H11 supports the significant difference in the take-off height between different take-off substrates ($F=2.770$, 3 d.f., $P<0.05$). Gibbons take-off from a tree trunk if the take-off height is 6-10m. The large branches are used when taking-off from lower heights, of 6-10, 11-15 and 16-20m (and the exception of 31-35m), and not used much when taking-off from higher heights of 26-30 and 21-25m. Small branches are used at heights of 21-25 and 26-30m, probably due to the fact that this would enable a longer distance to be crossed if at the end of the branch rather than the middle of the tree **(Figure 3.17)**. As for landing substrates, ***H12*** supports the significant difference in the take-off height also ($F=4.299$, 3 d.f., $P<0.05$). The gibbons will use a different take-off height if landing on a small branch, compared to a tree trunk, and will do the same with a large branch and a tree trunk. Gibbons' height of take-off is affected by the type of substrate on which they will be landing **(Figure 3.18)**. The small branches and (less so) tree trunks appear to be favoured over large branches when landing on very low supports (6-10m), probably as there is little other choice. In general, tree trunks are used less at higher heights (with the exception of 31-35m which was most likely a tall emergent tree) and used more at the lower heights.

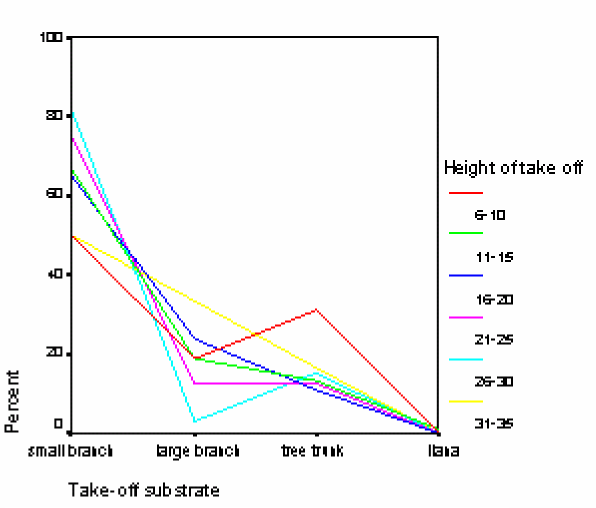


Figure 3.17 Percentage heights of take-off between different take-off substrates

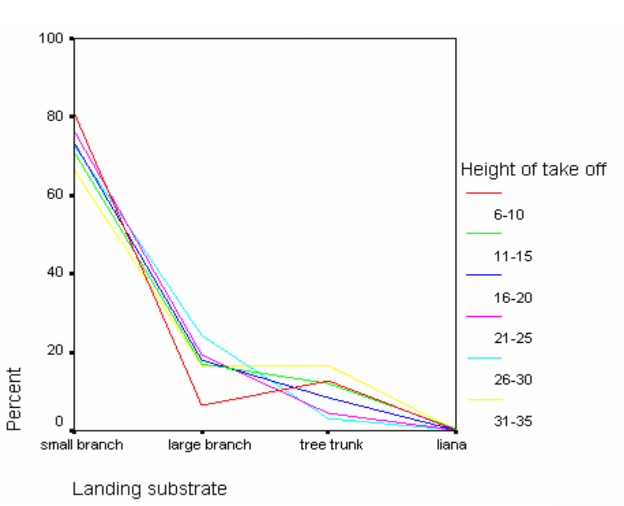


Figure 3.18 Percentage heights of take-off preferences different landing substrates

H13 supports no significant difference in take-off substrates between different forest types (F=0.595, 3 d.f., P>0.05), suggesting that gibbons are using the same take-off substrates regardless of the type of forest. There appears to be a slight preference for taking-off from tree trunks in broken canopy over the use of this substrate in gaps. Lianas were used over all other substrates in gap areas, although there was no significant difference **(Figure 3.19)**. As for landing substrates, ***H14*** again presents no significant difference (F=0.654, 3 d.f., P>0.05), suggesting that landing substrates are selected regardless of the type of forest. Although these data were not significant, the gibbons appear to have a mild preference for landing on large branches in broken canopy, rather than any other substrate **(Figure 3.20)**. Tree trunks were not popular for landing in broken canopy, but they were used for take-off **(Figure 3.19)**. Tree trunks were used for landing in the presence of gaps, probably due to the increased exposure, distance of travel and the need for a strong support. Lianas had a small sample size (n=2), thus making these data uneven.

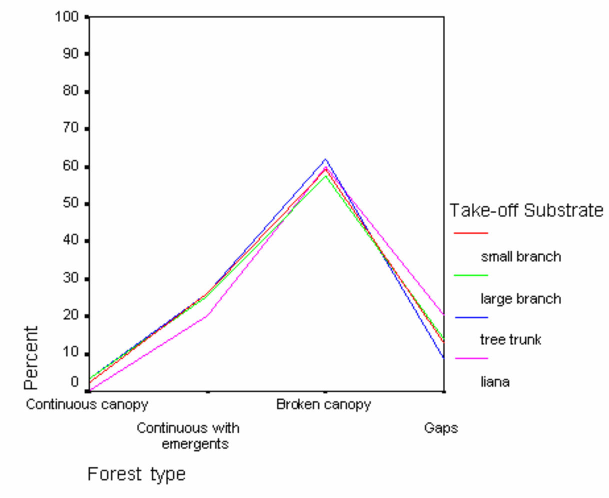


Figure 3.19 Percent of take-off substrates between different forest types

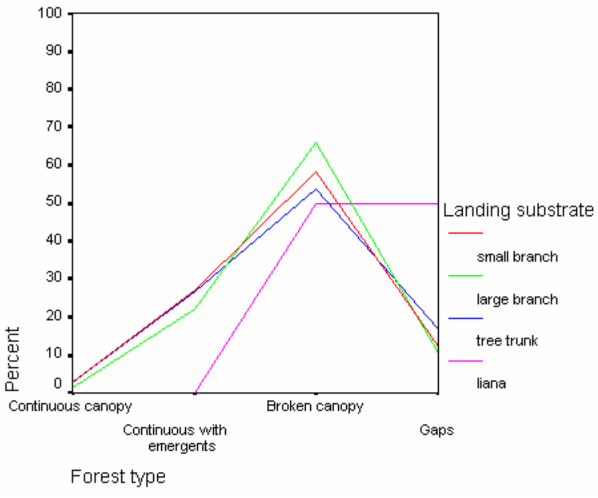


Figure 3.20 Percent of landing substrates between different forest types

3.2.1 Summary

In sum, the results of these hypotheses indicate that small branches are the most-used substrate in both take-off (68%) and landing (73%) ***(H10)***. In a study by Mittermeier (1978), brachiation in two *Ateles* species was measured between different substrate types. These were broken down into similar categories used in this study; bough (diameter ≥10cm), branch (diameter ≥2cm ≤10cm) and twig (diameter ≤2cm). Brachiation was exhibited in *A. geoffroyi* 3% of the time on boughs, 84% on branches and 13% on twigs. In *A. paniscus*, 3% of the time on boughs, 70% on branches, and 27% on twigs. Both species appear to be favouring branches over the other substrates, which would be roughly equivalent to both small branches, (≤6cm) and large branches (≥7cm) in this study. This is roughly comparable, as the gibbons do use small branches most often and large branches are the second commonest choice. The substrate types are affected by the height of take-off ***(H11)*** and the height of landing ***(H12),*** but are not affected by forest type ***(H13*** and ***H14)***, but this is not consistent with certain lemur species, as they used smaller supports less frequently in better forest types (Dagosto and Yamashita 1998).

These tests show support for the hypothesis in terms of height of take-off and landing, but not for forest type, demonstrating the similar array of structures available in all forest types, as is supported in ***H1***, and the use of stronger, or more flexible supports depending on the height of travel.

3.3 Gaps as constraints

How do they solve the problems of crossing gaps – and does this constrain their use of canopy strata for travel?

Although all primary forest is continuously regenerating, unnatural (e.g. logging canals) and natural (e.g. tree-falls) gaps in the canopy can often lead to large areas of secondary growth in an otherwise pristine forest. These areas are causing detrimental changes to the raw structure of the forest, which may cause a knock-on effect to the locomotion of the arboreal primates using the habitat for travel (McGraw 1996). It has already been proved in ***H8*** and **Figure 3.14** that gaps appear to be avoided purposely and better forest types selected for travel, but sometimes gaps are too frequent to be avoided, as is demonstrated by group Ninja in **Figure 3.15**. Although this result was not significant, Ninja still appeared to show a preference for gap areas. All other groups have found a way around these constraints and this is explored by testing whether there were significant differences in the following hypotheses:

H15 – *Frequency of jump compared to swing.*
H16 – *Jumping and swinging behaviour between different individuals.*
H17 – *Distance travelled between jumping and swinging.*
H18 – *Height of take-off whilst jumping or swinging.*
H19 – *Distance travelled between each forest type.*
H20 – *Jump or swing behaviours between each forest type.*
H21 – *Take-off heights between each forest type.*

H15 supports the significant difference between jumping and swinging behaviours ($X^2=128.125$, 1 d.f., $P<0.05$). Brachiation (swinging) is more commonly used (66%) across all individuals **(Figure 3.21)**. This could be as it is a more energy-efficient mode of travel. ***H16*** also supports no difference between jumping and swinging behaviour across all individuals ($X^2=1.448.$, 1 d.f.., $P>0.05$), indicating that all individuals will jump and swing roughly the same amount, although swinging is the commonest behaviour found in all individuals **(Figure 3.22)**.

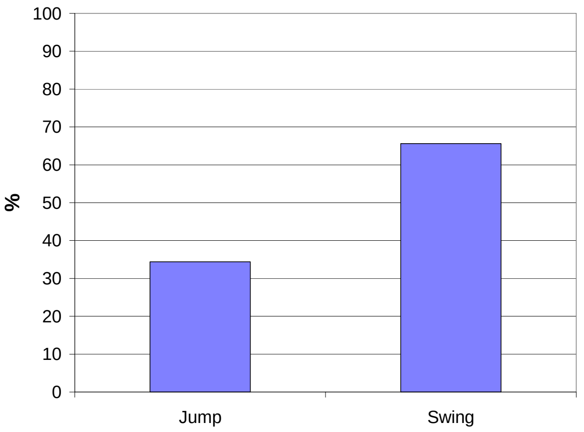


Figure 3.21 Frequencies of jumps (34.4%) and swings (65.6%) for all individuals in all forest types

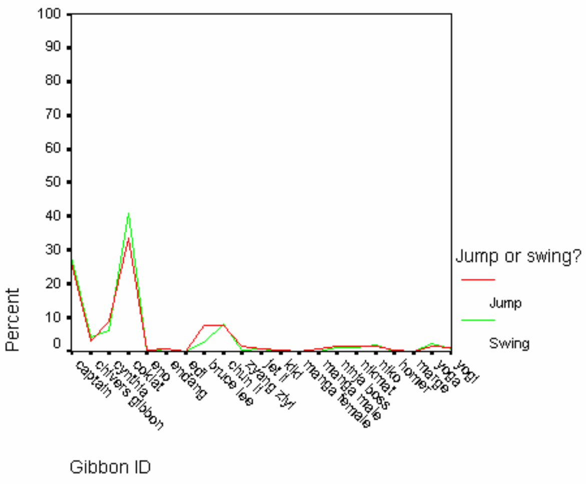


Figure 3.22 Jump and swing behaviours in each individual

H17 supports the significant difference in the distances travelled whilst jumping or swinging (X^2=81.762., 1 d.f., P<0.05). The gibbons have been shown to swing more often over shorter distances (1-4m) and to jump more over greater distances (5-9m). Where the lines cross, at about 4m, is where the frequency of jumping and swinging is about equal **(Figure 3.23)**. They are jumping rather than swinging to negotiate larger gaps; if, indeed, this is a more costly form of locomotion, then gaps are posing a problem in this instance. It has not been shown to be more or less costly regarding height of take-off, as ***H18*** supports no significant difference whilst jumping or swinging (F=0.143, 1 d.f., P>0.05), indicating there was no preference of locomotor behaviour at any take-off heights **(Figure 3.24)**.

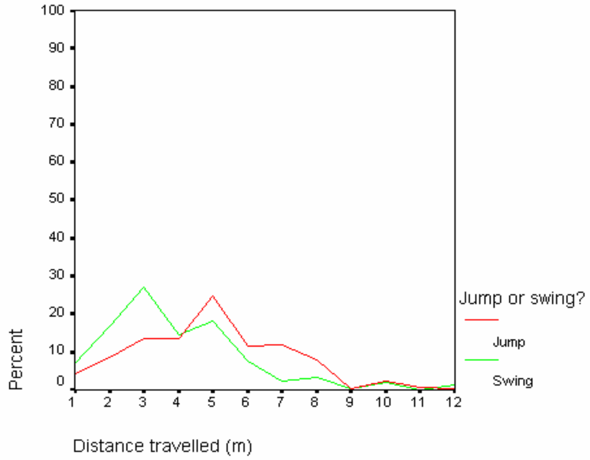


Figure 3.23 Jump and swing over different distances

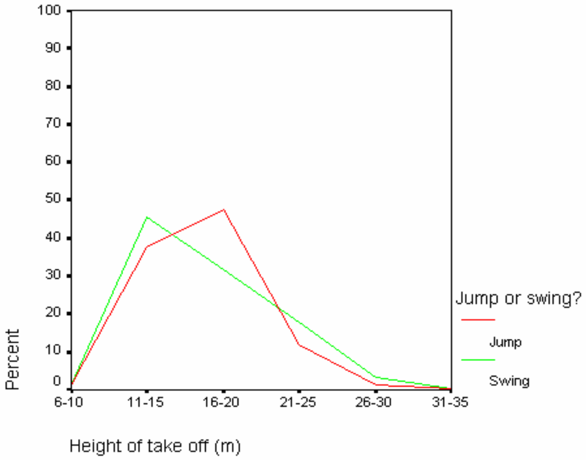


Figure 3.24 Percentage heights of take-off between jumping and swinging

H19 supports the significant difference in the distance travelled between each forest type (F=7.322, 3 d.f., $P<0.05$), but only between ‘continuous canopy’ and ‘broken canopy’ and also between ‘continuous with emergents’ and ‘broken canopy’. Forest types, ‘broken canopy’ and ‘gaps’ are not significantly different in the distance travelled. The gibbons are travelling differently, mainly in ‘broken canopy’. They do not travel differently in ‘gaps’ in comparison to any other type **(Figure 3.25)**. This suggests that gaps are not changing their locomotor behaviour in the distance-travelled sense, whereas broken canopy is, perhaps, caused by the inconvenience of having to change heights constantly in order to reach their destination. The median distance travelled, as shown in **Figure 3.26**, illustrates the short distances travelled in ‘broken canopy’ compared to all other types, suggesting that they are swinging more than jumping in order to conserve energy in these areas, and using less stable supports due to the area being composed of secondary growth.

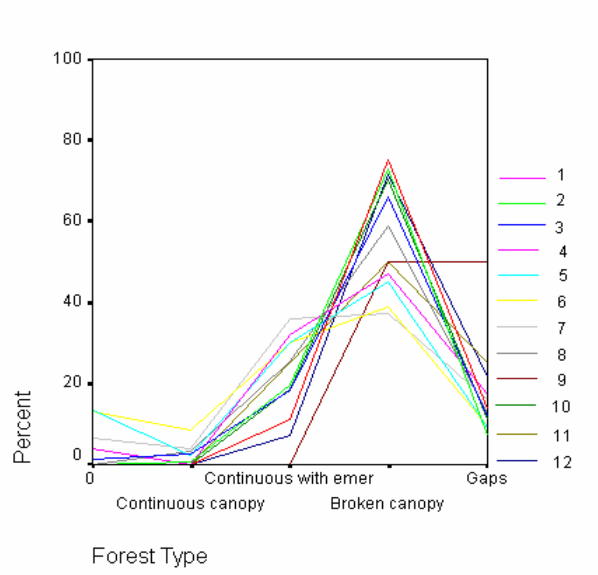


Figure 3.25 Percent of distance travelled between different forest types

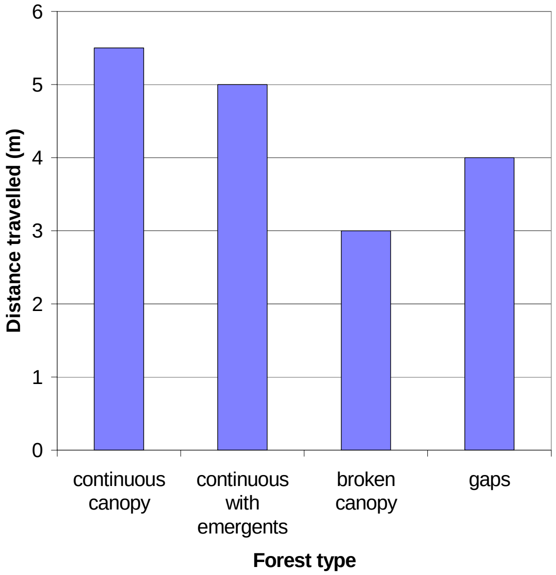


Figure 3.26 Median distance travelled in each forest type

H20 supports no overall significant difference in jumping or swinging behaviour between different forest types (F=2.591, 3 d.f., P>0.05) **(Figure 3.27)**. The gibbons are jumping and swinging differently in 'continuous with emergent canopy' compared to 'broken canopy', possibly a result of having to swing more often in 'broken canopy' to conserve energy in an uneven canopy environment, but the significant difference between these forest types is small (following a Tukey's *post-hoc* test, P=0.041).

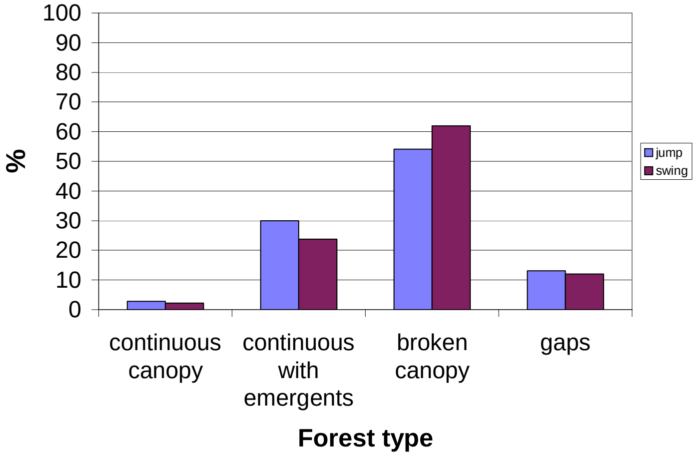


Figure 3.27 Percentage of jump and swings in each forest type

H21 supports the significant difference in take-off heights between the different forest types (F=11.440, 3 d.f., P<0.05). The effects that forest type can have on the take-off height of gibbons are shown in **Figure 3.28**. They jump from higher levels (21-25, 26-30 and 31-35m) rather than lower (6-10, 11-15 and 16-20m) when in 'broken canopy'. When encountering 'gaps' their preference appears strongly to be for either a very high (31-35m) or very low height (6-10m), thus implying the lack of available mid-level structure heights. The same data are shown in a different way in **Figure 3.29**. In 'continuous with emergent canopy', there is a strong contrast with 'gaps'. With 'gaps', the gibbons either jump from a high (31-35m), or a low (6-10m) height. With 'continuous with emergent canopy' they jump at the mid-level heights (11-15, 16-20, 21-25 and 26-30m), proving the lack of available intermediate height structures in 'gap' areas, and the presence of it in 'continuous with emergent canopy'. Following a Tukey's *post-hoc* test, 'continuous canopy', 'continuous with emergent canopy' and 'gaps' were all significantly different to 'broken canopy' (P<0.05). All other take-off heights were not significantly different in all other forest types (P>0.05).

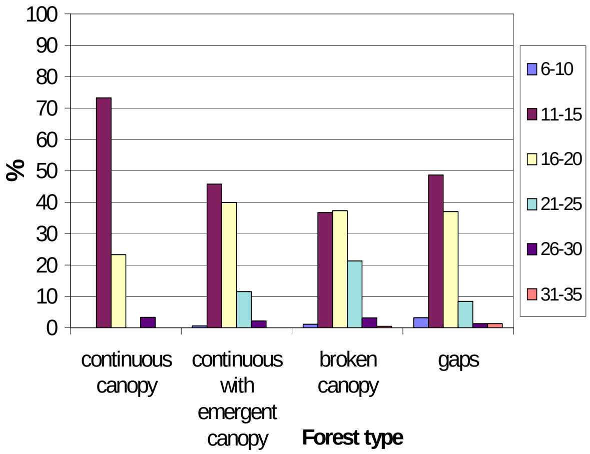


Figure 3.28 Percentage heights of take-off between forest types

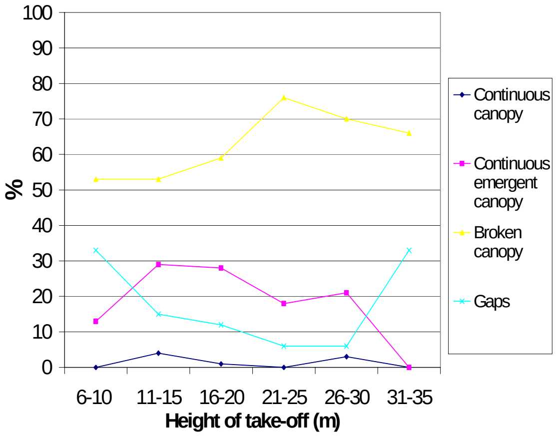


Figure 3.29 Percentage heights of take-off in each forest type

3.3.1 Summary

In sum, the results of these hypotheses indicate that brachiation is, generally, the commonest form of travel ***(H15)*** and all individuals share this preference ***(H16)***. This is also the case with the siamang, who use brachiation as their primary form of locomotion (Fleagle 1976a). This is similar in other species, such as *Ateles,* who brachiate 26% (*A. geoffgoyi*) and 39% (*A. paniscus*) of the time, whilst jumping only 11% and 4%, respectively (Mittermeier 1978). Other locomotor behaviours, such as climbing (40%, 31%), bipedalism (0.8%, 0.7%) and quadrupedal walking (22%, 25%) were used the remainder of the time. Brachiation is used for travelling over shorter distances (mean – 3.96m) and jumping for longer (mean – 4.95m) ***(H17),*** but there appeared to be no preference of either across all take-off heights ***(H18)***. ***H17*** does not concur with Fleagle (1976a), where siamangs are brachiating over longer distances (mean - 6.26m) than they are jumping (mean - 3.95m). The gibbons travelled shorter distances in 'broken canopy' ***(H19)***, brachiated more frequently ***(H20)*** and jumped from high levels ***(H21)***. In a study by McGraw (1996), the locomotor behaviours of five cercopithecid monkeys were observed in disturbed and undisturbed habitats. As an example, *Colobus badius* brachiated 4.9% and jumped 16.9% in undisturbed habitats and in disturbed – 3.3% and 18.4%, respectively (there were five locomotor modes in total; climbing (17.6%, 16.7%), quadrupedal walking (53.6%, 52.8%) and quadrupedal running (6.9%, 8.9%)).

Similar to this study, there were no statistical differences in locomotor mode between habitats; the differences in substrate availability in all forest types did not affect the travel techniques of any monkey enough to cause a substantial change. These tests show support for the hypothesis of ways that the gibbons overcome the problems of crossing gaps; elements of their behaviour change in disturbed habitats, inevitably becoming more energetically costly, by means of continuous ascent and descent through the uneven canopy. Their use of canopy is compromised, sometimes finding no other alternative but to cross the gap. An interesting addition to this study would have been to compare the effects on natural and unnatural gaps. I did not possess the necessary data to analysis this, but would have made an interesting comparison between the impacts of natural compared to human influence on the status of the gibbons.

3.4 Different locomotor techniques

Are the gibbons using different locomotor techniques when encountering gaps?

In terms of energy expenditure, gibbons could potentially be using the least-costly form of locomotion to combat the problem of crossing gaps. This is explored by testing whether there were significant differences in the following hypotheses:

H22 *– Jump and swing behaviours between different take-off substrates.*
H23 *– Jump and swing behaviours between different landing substrates.*

H22 supports the significant difference in jump and swing behaviours between take-off substrates (X^2=76.359., 1 d.f., $P<0.05$). The gibbons appear to prefer to take-off with a jump from a tree trunk **(Figure 3.30)**. They swing to take-off from small branches, but jump to take-off from large branches. With regard to the compliance of the substrate, this indicates they would rather swing over small distances and jump over larger ones, as described in ***H17***. As for landing substrates, ***H2*** also supports a significant difference in jump and swing behaviours (X^2=13.513., 1 d.f., $P<0.05$). The gibbons appear to prefer strongly to land a jump on a tree trunk. They will appear to prefer landing swings on large and small branches. Jumping appear to be the overall preferred locomotor technique when using tree trunks as supports for both take-off and landing **(Figure 3.31)**. This is probably caused by the fact that gibbons use jumping for long distances and the tree trunk is the strongest support available.

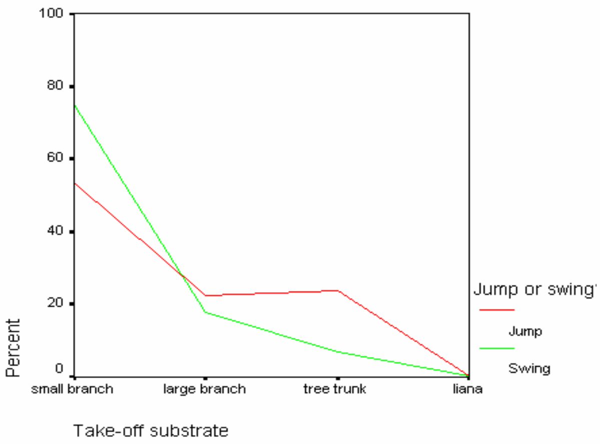


Figure 3.30 Percentage jump and swing between different take-off substrates

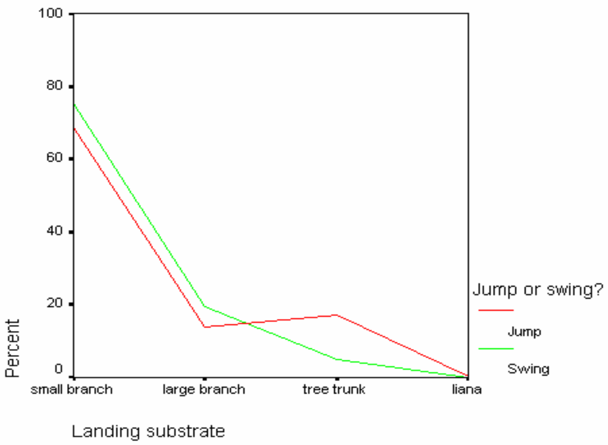


Figure 3.31 Percentage jump and swing between different landing substrates

3.4.1 Summary

In sum, the results of these hypotheses indicate that, as ***H17*** shows, brachiation is used more over shorter distances. The gibbons appear to prefer taking-off with jumps from strong supports (tree trunks and large branches) and swinging from weaker supports (small branches) ***(H22)***. A correlation is seen with the landing substrates, only they are landing swings rather than jumps on large branches ***(H23)***. Mittermeier (1978) states that jumps in *Ateles* take-off and land from all substrate types, but twigs are particularly important for landing (55%) rather than take-off (27% of all observations). The same pattern is shown in this study with the jumps landing on small branches 68% of time, whilst taking-off from them 52% of time. Boughs were more commonly used for take-off (23%) than landing (17%), as they were in for jumps this study; 22% (take-off) and 16% (landing). Fleagle (1976a,b) shows siamang and lar gibbons to brachiate 57% and 62%, respectively, of the time from a bough (diameter ≥10cm, equivalent to a point between a small (≤6cm) and large branch (≥7cm) in this study), whilst only using it for jumping 23% and 6% of the time. Fleagle (1976a,b) did not fully differentiate between take-off and landing substrates, but his study animals did appear to use small branches a lot less than the gibbons in Sebangau, perhaps due to the forest being of a better quality, with a greater abundance of large trees. ***H20*** shows their locomotion is altered in 'broken canopy' – they are possibly brachiating more in this habitat in order to conserve energy by using smaller distances ***(H19)*** and small branches ***(H24)*** for travel to maximise the distance able to cross.

3.5 Stability of substrate

How does the stability of the substrate relate to preference of use in crossing gaps?

As is demonstrated previously in this chapter, substrate types are affecting certain locomotor behaviours ***(H11*** and ***H12)***. As they are already affecting the take-off and landing heights, then it is reasonable to assume that they will have an effect on the distances travelled. This is explored by testing whether there were significant differences in the following hypotheses:

H24 – *Distance travelled between different take-off substrates.*
H25 – *Distance travelled between different landing substrates.*

H24 supports the significant difference in the distance travelled between take-off substrates (X^2=52.636, 11 d.f., $P<0.05$). The gibbons' travel distances vary, depending on the type of substrate from which they take-off. They are more likely to take-off from small or large branches for short travel distances (3m), large branches for medium travel distances (5m), tree trunks for long distances of about 8m and back to the use of large branches for very long distances of 9 – 12m, probably so that they can move away from the centre of the tree to maximise the crossing distance. The liana substrate was infrequently used, hence the small sample size (n=5), but was used only for distances under 4m, probably due to the inconsistent instability of the supports **(Figure 3.32)**. In general, gibbons will use stronger supports (large branches or tree trunks) for longer distances and less stable supports (small branches and lianas) for shorter distances. This pattern is similar for landing substrates, as ***H25*** also supports the significant difference in the distance travelled (X^2=29.597, 11 d.f., $P<0.05$). In correlation with the take-off substrates, the gibbons are more likely to land on small branches for short travel distances (3m), large branches for medium travel distances (5m), tree trunks for long distances (6-11m) and back to large branches for 12m distances **(Figure 3.33)**. The lianas have a very small sample size (n=2), but are still only used if landing a jump under 4m. Median distances travelled for each substrate type are shown in **Figure 3.34**.

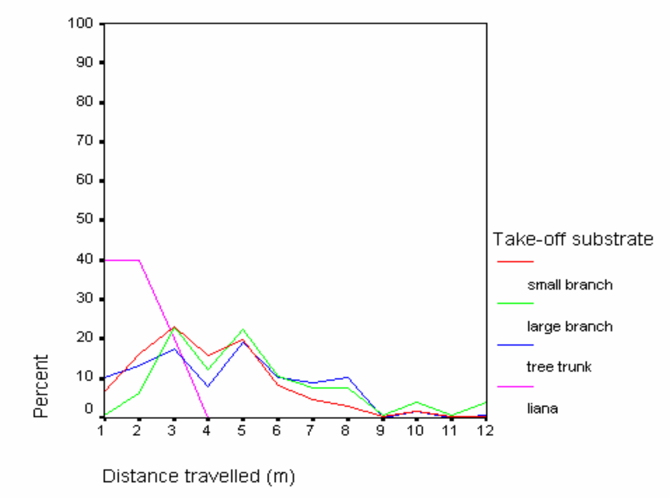


Figure 3.32 Percentage use of take-off substrates in relation to distance travelled

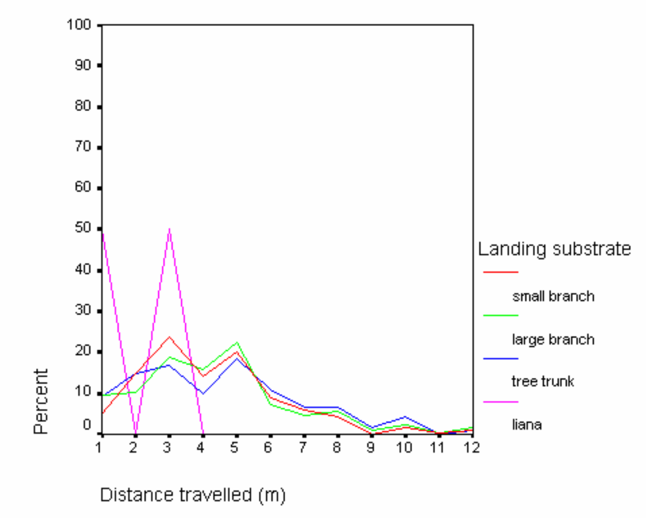


Figure 3.33 Percentage use of landing substrates in relation to distance travelled

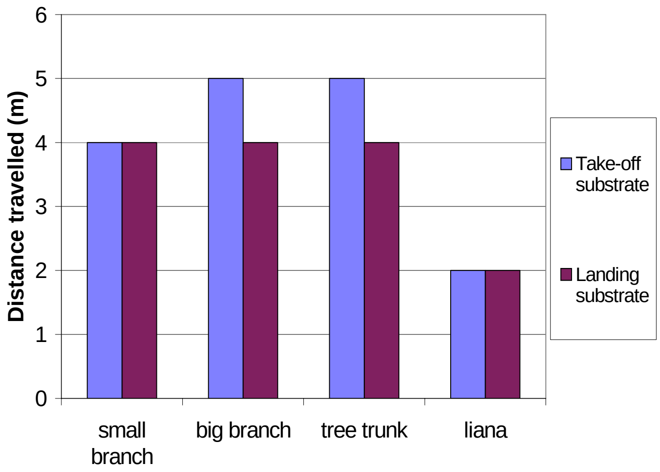


Figure 3.34 Median distance travelled for each substrate type

3.5.1 Summary

As is already established in ***H10***, small branches are by far the commonest used substrate. ***H13*** and ***H14*** show that they are used regardless of forest type. ***H22*** and ***H23*** illustrate that stronger substrates are used for jumping and weaker substrates are used for swinging. Stronger supports are used for taking-off for longer distances and weaker supports for shorter distances ***(H24)***, and this is reflected by the landing substrates also

(H25). Gaps pose a problem, as they either present a very large discontinuity or a succession of smaller discontinuities (uneven canopy); the gibbons have a choice to either take the risk of travelling across the large gap or going around the longer way, but sometimes they have no other option but to choose the former. This is energetically costly for them, as efficient travel through the canopy, in terms of reducing distance of direct travel between two points, is heavily constrained by the presence of gaps (Cannon and Leighton 1994).

3.6 Energy efficiency in travel

Is jumping or swinging a more energy-efficient mode of travel?

All exertions by muscles, whether to resist external forces or to produce movement, impose a certain energetic cost (Alexander 1968). It would thus make sense for selection to decide on strategies of movement that aim to minimise the metabolic cost of locomotion (Crompton *et al.* 1993). Some authors regard bimanual suspension (brachiation) as the most energy-efficient mode of travel (Preuschoft and Demes 1984; Usherwood and Bertram 2003); 80% of *H. lar* travel modes recorded by Andrew and Groves (1976) were by brachiation, compared to 50% for siamang (Fleagle 1976a) and 66% for agile in this study.

This indicates that brachiation is the most energy-conserving of all travel modes, as it would make evolutionary sense for the animals to travel the least costly way possible most of the time. Cant (1986) hypothesises that suspensory locomotion in spider monkeys (*Ateles*) decreases energy costs per unit of distance travelled. It was demonstrated with a captive spider monkey by Parsons and Taylor (1977) that suspensory locomotion costs more than quadrupedal locomotion per unit *time*, although the former is the faster form of movement. Only if the spider monkey maintains a good speed by suspensory locomotion, can it travel at a lesser energetic cost than slower quadrupedal movement, although this has yet to be tested thoroughly (Cant 1986). The cost of locomotion in any given species is a combination of the distance travelled and the specific mode of locomotion used, rather than pace or time spent moving (Taylor *et al.* 1970).

Jumping involves reasonably large forces, when compared to other locomotor activities (Crompton *et al.* 1993). Furthermore, it is not a cyclical activity, like brachiation, so there is no opportunity to conserve potential energy. These facts indicate jumping to be an energetically-costly form of locomotion (Taylor *et al.* 1982; Walton and Anderson 1988). As it is a ballistic travel mode, there is a certain angle (45º), which maximises the efficiency of the jump, and tests on captive prosimians (*Galago moholi*) support this, by following the expectation for optimal energy-efficiency (Crompton *et al.* 1993). Tree-sway in orang-utans was studied by Thorpe *et al.* (2007) with regard to energetic cost. Jumping was found to be more than half as costly as tree-swaying, as was ascending and descending to cross the discontinuity. Pontzer and Wrangham (2004) tested the arboreal-terrestrial trade-off in chimpanzees and, particularly, whether arboreality is a strategy for reducing the energetic costs of locomotion by decreasing the time spent climbing. Their results demonstrated that about ten times more energy is spent each day on terrestrial travel than on climbing. They concluded that there must be other beneficial factors, such as avoidance of falls from the tree-tops, which encourage this energetically-costly adaptation. If taken in regard to which mode is preferred when crossing gaps, perhaps a conclusion can be drawn from these hypotheses:

3.6.1 Summary

It has been observed in ***H15*** that swings are used more over jumps in this study and this is constant across all individuals ***(H16)***. Jumping is used more over longer distances and swinging over shorter ***(H17)***. ***H22*** and ***H23*** illustrate that jumping and swinging behaviours are restricted by substrate type, jumping and strong supports whilst swinging and weaker supports. It would be feasible to say that weaker supports are more costly energetically than stronger ones, mainly due to their flexibility. Gibbons are losing potential energy when they let go of a small branch as it pings back, releasing the energy that the gibbon would have used. Stronger supports do not do this, they are more stable and, thus, more energy is passed onto the gibbon. Perhaps gibbons are trying to counter-act this cost with brachiation rather than jumping, as this will equalise the impact on their energy stores.

Another theory as to why gibbons are swinging rather than jumping shorter distances is because it makes sense for the individual to travel longer distances in brachiation sequences, than it does to stop and start as the animal will lose momentum, and thus energy. A 3.9m distance is the average for swings, indicating that the gibbons were exhibiting behaviour that would enable as much energy to be conserved as possible.

Brachiation is potentially less energetically costly than jumping and ***H20*** poses the question; does jumping or swinging differ between forest types? If there is no difference then locomotion is not restricted by forest type, thus meaning each forest type has the same potential energy cost, but if they are using swinging over jumping more in a particular forest type, then it might be assumed more energetically efficient. This inclination is apparent only in ‘broken canopy’ and not in any other type **(Figure 3.27)**, suggesting they are brachiating more to conserve energy when in areas of uneven, regenerating forest. Gaps no doubt represent a large problem, but gibbons are adapting to these areas and finding a way around them. It is only when the gaps begin to regenerate and secondary growth occurs that the gibbons will again be presented with a problem.

3.7 Body size as a restricting factor for travel

Do body size and the presence of infants ventrally restrict travel in the canopy?

Positional behaviour has already shown a wide degree of intra-specific variation due to age, sex, and season in which data were collected (Crompton 1984; Sugardjito and van Hooff 1986; Doran 1993; Gebo and Chapman 1995). The various locomotor and postural capabilities of smaller individuals enable them to use different features of the habitat from larger-bodied individuals. This variety of capabilities within the group should be important when assessing the effect of resource availability on the species (Fleagle 1976b).

It has been shown in many studies that there are distinct differences in locomotor techniques because of body size. Doran (1993) demonstrated, using chimpanzees, that body size differences can be directly related to differences in travel techniques; smaller females are more arboreal than the larger males, although these differences obviously vary greatly between species. Differences in travel techniques across species seem to mirror the differences in body weight (Crompton 1984). Fleagle and Mittermeier (1980) also agree that the size of a species (of Surinam monkey) undoubtedly correlates with the locomotor behaviour; a larger-bodied animal will climb more and leap less.

This draws a negative parallel (assuming males and females differ in body size) with Chatani (2003), who discovered that Japanese macaque males prefer to leap more frequently and further than females. Females were also more arboreal than males. These differences between the sexes are regarded to be correlated with a number of factors, including food choice, morphology, social activity and the presence of infants. Sex-differences also occurred in the Sumatran orang-utans; adult males differed significantly to females with infants and adolescents with regard to locomotor types and substrate use. The results of the study by Sugardjito and van Hooff (1986) indicated that larger-bodied individuals will travel at lower canopy heights due to constraints of body size. Females with infants also travel at lower heights, but rest at higher levels, suggesting that they travel at lower heights regardless of a greater risk of predation.

Decreased travel efficiency can potentially make energy balances more negative, possibly affecting reproduction and the population’s long-term viability. Thus, it is important, to test if females with infants ventrally and younger animals are being affected adversely by this. This is explored by testing whether there are significant differences in the following hypotheses:

H26 *– Height of take-off between age-classes.*
H27 *– Height of take-off between sexes and females with infants ventrally.*
H28 *– Height of landing between age-classes.*
H29 *– Height of landing between sexes and females with infants ventrally.*
H30 *– Distance travelled between age-classes.*
H31 *– Distance travelled between sexes and females with infants ventrally.*
H32 *– Jump and swing behaviours between age-classes.*
H33 *– Jump and swing behaviours between sexes and females with infants ventrally.*
H34 *– Use of take-off substrates between age-classes.*
H35 *– Use of landing substrates between age-classes.*
H36 *– Use of take-off substrates between sexes and females with infants ventrally.*
H37 *– Use of landing substrates between sexes and females with infants ventrally.*

H26 supports no significant difference in the heights of take-off between age-classes (F=1.182, 3 d.f., P>0.05). The adults, adolescents and juveniles seem to follow the same pattern of canopy use for take-off **(Figure 3.35)**. The small sample size (n=1) for the infant does not tell much about its movement patterns, as only one jump was ever recorded. In this instance body size is not a factor limiting take-off height. As for the sex-classes, ***H27*** does support a significant difference in the heights of take-off between the sexes and females with infants ventrally (F=12.131, 3 d.f., P<0.05). Females with infants ventrally are typically taking-off from lower heights (11-15m) than males, who are taking-off from heights of 16-20m, and females, who equally prefer to take-off from heights of 11-15 and 21-25m **(Figure 3.36)**. A Tukey's *post-hoc* test proves females with infants ventrally are significantly different to the male (P<0.05), but not to the female (P>0.05). This is an example of how behaviour can be changed as a result of carrying an infant; the females are less willing to take risks by jumping off higher heights. Disturbed forest supplies the forest with an uneven canopy for inefficient travel. If females are already taking-off from lower heights, whilst carrying an infant ventrally, then this further reduces their options for travel.

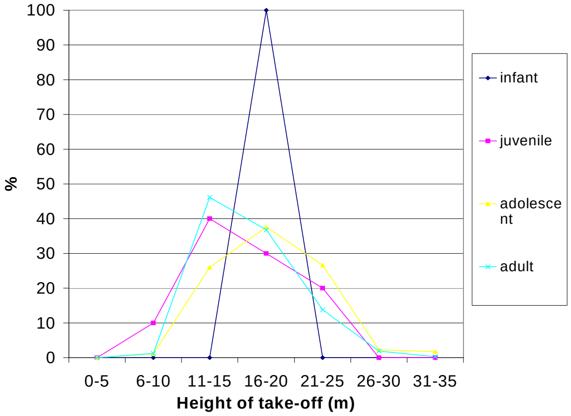


Figure 3.35 Percentage of take-off heights between age-classes

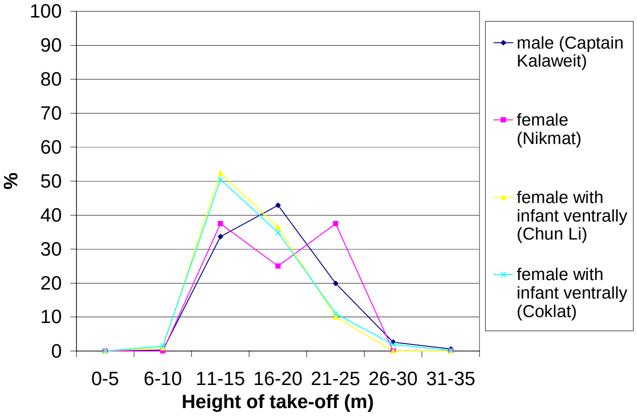


Figure 3.36 Percentage of take-off heights between sex classes and females with infants ventrally

H28 supports no significant difference in height of landing between age-classes (F=1.734, 3 d.f., P>0.05). Again, the age-classes are following the same pattern of canopy use for landing (note the small sample size (n=1) for the infant, **Figure 3.37**). Body size is not a limiting factor for landing height. Again, for the sex-classes, ***H29*** supports a significant difference in landing heights (F=8.451, 3.d.f., P<0.05). These data correlate with the take-off height data accordingly. Again, following a Tukey's *post-hoc* test, females with infants are significantly different to the male (P<0.05), but not to the female (P>0.05). Females with infants ventrally are landing at lower heights than males and females, probably because their take-off height is lower. The female is landing at lower heights than the male, but, in one instance, a female with an infant ventrally (Coklat) landed at higher heights of 21-25m than the male and the female **(Figure 3.38)**. Landing heights are not as fundamentally important to this study, as they just draw a parallel with take-off height data.

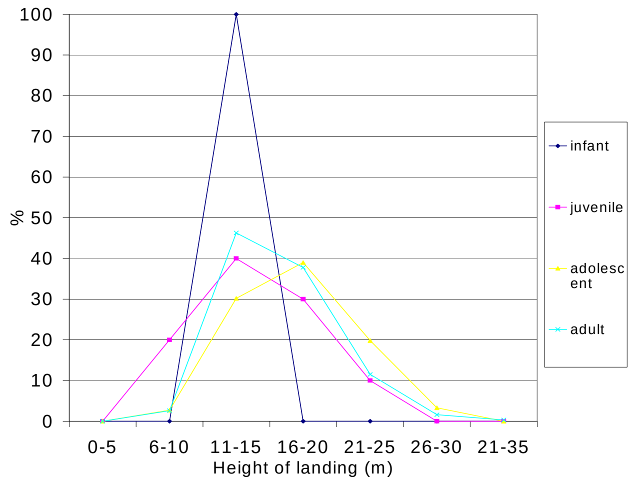


Figure 3.37 Percentage of landing heights in different age-classes

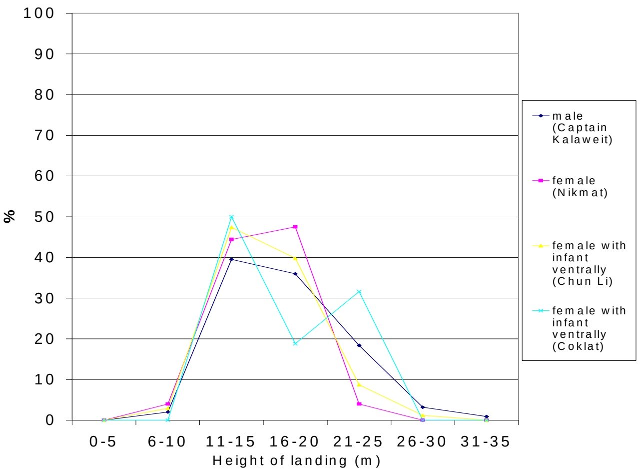


Figure 3.38 Percentage of landing heights between sex classes and females with infants ventrally

H30 does support a significant difference in the distance travelled between age-classes (X^2=29.406, 11 d.f., $P<0.05$). Juveniles are generally travelling shorter distances (apart from a one-off at 12m) than adolescents or adults. Adolescents follow a similar pattern to adults, but travel more often over distances of 1-2m, whereas adults will travel more often over distances of 3-8m **(Figure 3.39)**. This is a case where body size has been proved to be a limiting factor. Smaller individuals will normally jump over smaller distances than larger-bodied, more-able individuals. ***H31*** also supports a significant difference between the sex-classes (X^2=30.263, 11 d.f., $P<0.05$), but only between the male and one of the females with an infant ventrally (Coklat). Females with infants ventrally did not travel as far as either the males or the female. They tended to travel shorter distances, most commonly either 3 or 4m. The male was the one who travelled the furthest, with distances commonly of 8, 10 and 12m **(Figure 3.40)**. This is an example of how carrying an infant ventrally can change certain behaviours and, in this instance, jump less risky distances.

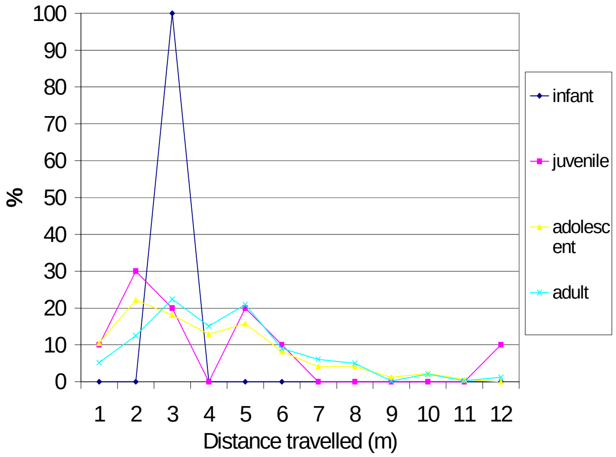


Figure 3.39 Percentage of distance travelled between age-classes

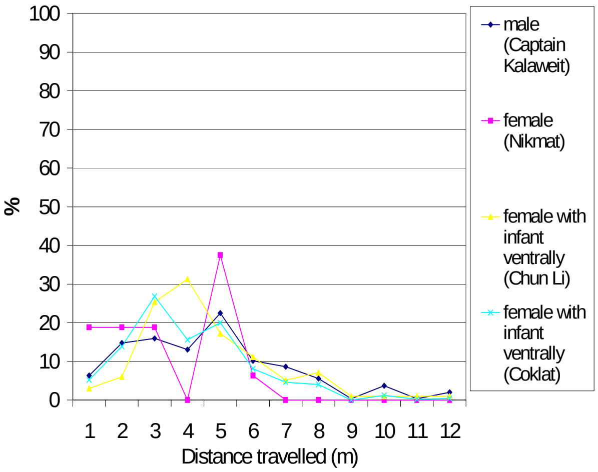


Figure 3.40 Percentage of distance travelled between sex-classes and females with infants ventrally

H32 supports no significant difference between swinging and jumping between age-classes (X^2=1.460., 1 d.f., P>0.05). Brachiating (swinging) is by far the most commonly-used mode of travel and this is consistent across all ages **(Figure 3.41)**. The same result is also supported by ***H33*** between sex-classes or females with infants ventrally (X^2=1.012., 1 d.f., P>0.05). Brachiation has also proven to be consistent across all sex-classes **(Figure 3.42).**

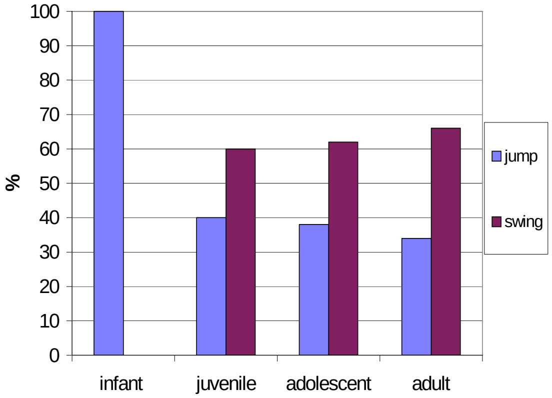


Figure 3.41 Distribution of jumps and swings for each age-class

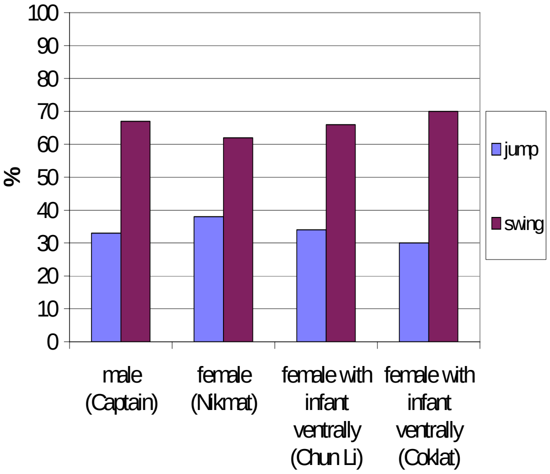


Figure 3.42 Distribution of jumps and swings for each sex-class and females with infants ventrally

H34 supports the significant difference in the take-off substrate preference between age-classes (X^2=20.486, 3 d.f., P<0.05). Small branches were used more frequently as age increased, tree trunks were used more frequently as age decreased and large branches were relatively consistent across all ages **(Figures 3.43)**. In ***H30*** it states that juveniles travel over smaller distances than adolescents or adults. This may be why they more commonly use tree trunks for take-off; it is a stable support and a 'safer' place to release from than a weak small branch. These young animals are still learning about support stability and are perhaps more cautious than the older ones. In this instance body size is a limiting factor. ***H35*** also supports this for landing substrate (X^2=13.710, 3 d.f., P<0.05). Adolescents are using large branches more and smaller branches less than either juveniles or adults. Landing on tree trunks is relatively consistent across all ages, probably due to the stability of the support. Juveniles are landing more on smaller branches than adolescents and adults **(Figure 3.44)**. Perhaps to get the furthest distance possible, they are reaching the terminal branches of trees instead of the larger branches, due to a reduced body size compared to the older individuals. Body size is, again, a limiting factor.

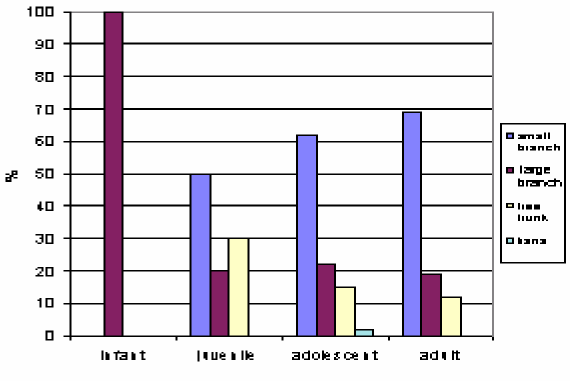


Figure 3.43 Differences in take-off substrates between age-classes

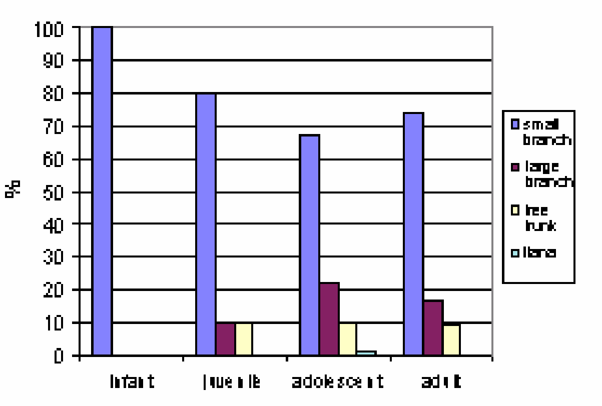


Figure 3.44 Differences in landing substrates between age-classes

H36 supports no significant difference in the take-off substrates between sex-classes (X^2=5.712, 3 d.f., P>0.05), thereby suggesting that there is a relatively consistent use of substrates across all sexes **(Figure 3.45)**, but ***H37*** supports a significant difference in the landing substrates between sex-classes (F=2.749, 3 d.f., P<0.05). Following a Tukey's *post-hoc* test, only the male (Captain) and female with an infant ventrally

(Coklat) were significantly different, the male landed more on large branches, whereas the female more on small branches **(Figure 3.46)**.

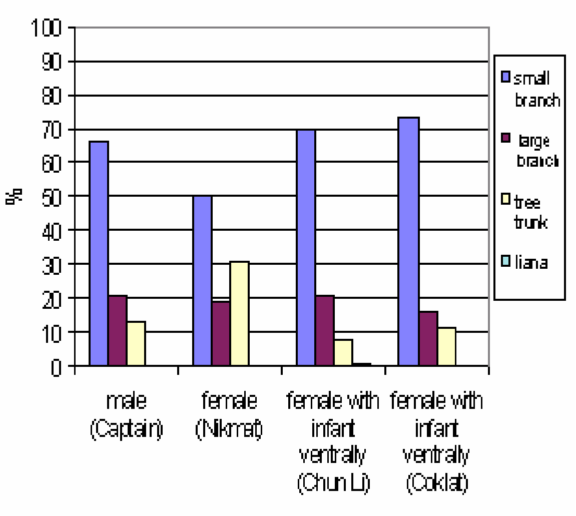


Figure 3.45 Differences in take-off substrates between sex-classes

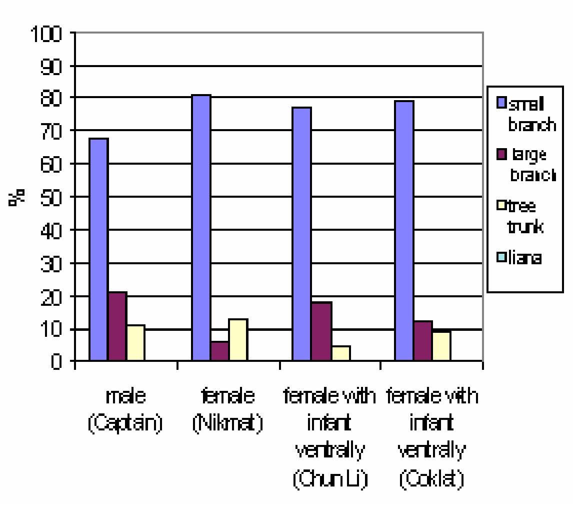


Figure 3.46 Differences in landing substrates between sex-classes

3.7.1 Summary

In sum, the results of these hypotheses indicate that, all age-classes follow the same pattern of canopy use with regard to take-off ***(H26)*** and landing ***(H28)*** heights, but with regard to sex-class, females with infants ventrally are taking-off ***(H27)*** and landing ***(H29)*** at lower heights than the male (but not the female). Distances travelled were different between age-classes, with younger individuals crossing shorter distances ***(H30)***, and females with infants ventrally also crossing shorter distances than males ***(H31)***. Jumping and swinging was constant between both age ***(H32)*** and sex-class ***(H33)***. The use of substrates between ages is different for both take-off, where older individuals are more inclined to use weaker supports and younger individuals to use stronger supports ***(H34)***, and for landing, where younger individuals are using weaker landing supports than older individuals ***(H35)***.

Clutton-Brock (1973) tested substrate use whilst feeding and resting between age-classes for red colobus (*Procolobus badius*) and the results showed that younger individuals used weaker supports than older individuals and only a few differences existed between the males and females. These findings concurred with a study by Kummer (1971) on hamadryas baboons (*Papio hamadryas*), whereby females fed in the terminal branches more than males due to their smaller body mass. This also enabled a reduction in food competition and an escape from male harassment. That adolescent colobus were able to use weaker substrates than the heavier adults did not necessarily restrict the adults' selection of food, as they could use their larger bodies for strength in bending, and their longer arms to reach further out to food on weaker supports.

For the sexes, take-off substrates are used consistently across all sexes ***(H36)***, but for landing substrates, just one of the females with an infant ventrally used small branches more, whereas the male used large branches more ***(H37)***. In a study by Remis (1995) gorilla substrate preference was assessed, to conclude that small branches were chosen rarely by silverback males and, overall, females used smaller substrates than did males. There were a number of factors other than body size that influenced substrate choice, including group size, social rank and canopy structure. There is obviously a higher degree of sexual dimorphism between gorillas and gibbons, but this shows how each species can be different.

Comparable to Remis (1995), a study by Gebo and Chapman (1995) was carried out on five sympatric Old World monkeys. All five species studied appeared to prefer medium-sized supports, regardless of body size or structural availability, and positional behaviour did not differ between the sexes. This is also the case regarding three species of tamarin monkey, whereby all species used very similar positional behaviours (Garber 1991).

Overall, these outcomes show how body size can be a constraint for gibbons in some cases, and also females carrying infants are restricted in certain aspects of travel. This could prove a problem, but they are only different from the male and never significantly different from the female, so this could possibly be simply caused by the slight increase in body (muscle) mass and the differing social roles a male has to perform. These results support these hypotheses to show how body size can be restricting in some aspects of locomotion.

3.8 Summary of results

3.1 Selection of canopy heights and forest types for travel

There were significant differences found in:
***H2* –** *Canopy heights used by all groups.*
***H3* –** *Use of canopy height between different group territories.*
***H4* –** *Canopy height availability in all group territories.*
***H5* –** *Canopy height availability between different group territories.*
***H6* –** *Forest type used by all gibbon groups.*
***H8* –** *Forest types available to all gibbon groups.*
***H9* –** *Forest types availability between different group territories.*

There were no significant differences found in:
***H1* –** *Canopy height between different forest types.*
***H7* –** *Use of forest type between different group territories.*

3.2 Different variables of forest structure

There were significant differences found in:
H10 *– Frequency of use of different substrates.*
H11 *– Height of take-off between different take-off substrates.*
H12 *– Height of take-off between different landing substrates.*

There were no significant differences found in:
H13 *– Preference of take-off substrates between each forest type.*
H14 *– Preference of landing substrates between each forest type.*

3.3 Gaps as constraints

There were significant differences found in:

H15 – *Frequency of jump compared to swing.*

H17 – *Distance travelled between jumping and swinging.*

H19 – *Distance travelled between each forest type.*

H21 – *Take-off heights between each forest type.*

There were no significant differences found in:

H16 – *Jumping and swinging behaviour between different individuals.*

H18 – *Height of take-off whilst jumping or swinging.*

H20 – *Jump or swing behaviours between each forest type.*

3.4 Different locomotor techniques

There were significant differences found in:

H22 – *Jump and swing behaviours between different take-off substrates.*

H23 – *Jump and swing behaviours between different landing substrates.*

3.5 Stability of substrate

There were significant differences found in:

H24 *– Distance travelled between different take-off substrates.*

H25 – *Distance travelled between different landing substrates.*

3.7 Body size as a restricting factor for travel

There were significant differences found in:

H27 – *Height of take-off between sexes and females with infants ventrally.*

H29 – *Height of landing between sexes and females with infants ventrally.*

H30 – *Distance travelled between age-classes.*

H31 – *Distance travelled between sexes and females with infants ventrally.*

H34 – *Use of take-off substrates between age-classes.*

H35 – *Use of landing substrates between age-classes.*

H37 – *Use of landing substrates between sexes and females with infants ventrally.*

There were no significant differences found in:

H26 – *Heights of take-off between age-classes.*

H28 – *Height of landing between age-classes.*

H32 – *Jump and swing behaviours between age-classes.*

H33 – *Jump and swing behaviours between sexes and females with infants ventrally.*

H36 – *Use of take-off substrates between sexes and females with infants ventrally.*

CHAPTER 4 – CONCLUSIONS

In this study, many aspects of locomotion have been assessed in relation to impacts from the environment. Some of these have had a greater impact than others, and all have been explored in detail. The most fundamental question here is whether habitat disturbance is changing the locomotor behaviour of gibbons and, if so, to what extent.

There has been evidence for active selection of structure in a few previous studies (e.g. Cannon and Leighton 1994; McGraw 1996). It makes sense for an animal to choose the most efficient, direct route of travel, an act that can be loosely regarded as a preference (i.e. to use more than predicted based on abundance). It has already been established that gibbons travel through arboreal highways (Chivers 1974), which they assumedly choose with regard to their directness and structural appropriateness for travel. In a few instances, I witnessed gibbons jumping over very large gaps either to reach a favourite feeding tree or merely to cross a large discontinuity where there was no other choice. Gaps crossed this way represent a trade-off between high-energy and risk costs and the benefits from a greater directness of travel.

As areas with high levels of disturbance (be it natural or un-natural) produce an uneven canopy for travel, gibbons must alter their original behaviour to incorporate either more ascends and descends, or large, risky jumps across gaps, to reach a point, when they would have otherwise behaved naturally. These behavioural alterations must have some effect on their energy balances, in all probability, a negative one. Cannon and Leighton (1994) observed gibbons to jump twice as much during gap crossings than in normal travel and jumped more to cross wider gaps. The latter is consistent with this study – jumping was used more over longer distances than swinging, implying that the gibbons are using a higher-risk (and potentially more energetically-costly) mode of travel when confronted with the problem of large canopy gaps. This should not have to happen and the consequences of this problem are as yet unclear. A longer-standing study needs to be introduced to assess the long-term effects of habitat disturbance on this population.

Substrate choice was shown in this study to have an influence on heights of take-off and landing but not between forest types. The long-tailed macaques in Cannon and Leighton (1994) used more flexible, weaker substrates when crossing between trees, and were forced to cross from the terminal branches in order to maximise the potential distance that could be crossed. The gibbons in this study used small branches more than any other substrate. This is possibly due to their high frequency of availability, but also to maximise the crossing distance, as juveniles (the smallest body size) landed on small branches most commonly and took-off from tree trunks more than other age-classes. As gibbons mature, they are still testing out support strength and flexibility, thus the younger ones are being the most careful – taking-off and gaining maximum propulsion from strong supports and landing on the weakest with the greatest degree of flexibility, whilst, at the same time, maximising their travel distance. The habitat has proved to be relatively consistent in terms of canopy height in different forest types; thus, this should also stand true for consistency among substrate types. All trees have trunks, large and small branches, but some are more exposed than others; larger branches generally occur higher and small branches are usually to the periphery of the tree crown. In disturbed areas, trees are possibly more exposed and this is reflected in the study by a high percentage of tree-trunk use in gap areas.

As the study site was an old logging concession over 10 years ago, high levels of disturbance are still very apparent. Obviously, feeding trees are not going to grow conveniently in areas of undisturbed forest, they grow everywhere, thus forcing the gibbons into encountering gaps. Gaps have become a part of life for these gibbons and they will inevitably encounter them on a day-to-day basis. What is important now is to assess how they cope with these problems in the canopy and if they are causing a fundamental impact on their locomotor behaviour.

Firstly, it is crucial to establish their basic locomotor tendencies without the presence of gaps. We now understand they brachiate more than jump, and brachiation is generally over shorter distances than jumping. Their travel distances vary, depending on the substrate type from which they take-off and land – small branches for shorter travel distances. Heights of take-off were not a problem with regard to locomotor mode, but distance travelled was different in broken canopy. This is also the only forest type in which they brachiated more than jumped, suggesting a series of short, quick swings on small branches, which is the best way for dealing with an uneven canopy, where many ascents and descents must be made to reach the destination. It appears that they are skirting around the gaps, only sometimes taking the high-risk option of crossing the discontinuity.

Brachiation has been shown to be energetically less costly than jumping with regard to forest type. It makes evolutionary sense for selection to choose certain forms of movement that are more energy-conserving than others (Crompton *et al.* 1993). The opportunity to conserve potential energy is less in other forms of locomotion as they are not cyclical activities, thus momentum is lost, or never gained (Taylor *et al.* 1982; Walton and Anderson 1988). Gibbons are no doubt encountering gaps in the canopy, and adapting to them by means of exhibiting the least energetically-costly form of locomotion. This is advantageous to the species as a whole, as it shows that they are finding ways of dealing with pressures from disturbance and adapting their behaviours accordingly. Just because they have found a way to counter act the energy-costly impacts of disturbance, however, does not mean they are conserving as much energy as they would have if there was no disturbance. They are still having to 'go the long way round' instead of taking a direct travel route, simply because it does not exist. These impacts could possibly lead to a change in many aspects of gibbon behaviour.

One theory is that by expending more energy on combating the problem of gaps, less energy is available to be used on other things, such as calling, reproduction and lactation. They could potentially end up calling less, reducing the number of offspring in a lifetime and infant survival could decline. A similar notion was also theorised by Mather (1992) who believed more energy was spent on calling in hybrid gibbon pairs (*agilis* x *muelleri*) than pairs of the same species. The hybrid pairs sung more frequently, as they had to adjust to each others idiosyncrasies, thus less energy was available to be spent on reproduction, potentially causing the population to decline. These are all possibilities that could potentially threaten the survival of the species in the long-term. This is a reason why management plans for National Parks should be developed with gibbons in mind. If disturbance was to increase, and more gaps presented, then the effects could be detrimental. Gibbons could start coming to the ground instead of crossing gaps to reach a certain point, which could lead to increased problems with disease transmission, higher predation risks and vulnerability from human hunters. Feeding trees could become more dispersed and increased densities of particular foods could arise from disturbance (Johns and Skorupa 1987), making travel longer and more difficult for the animals, thus worsening the problem of energy expenditure.

Another theory is that gap presence could lead to an increase in group dispersal, in turn leading to more extra-pair copulations (EPCs) and further dispelling the notion that gibbons are monogamous. Proximity data would need to be analysed statistically to investigate this notion, but I witnessed the females from group Ninja, (which is particularly dispersed) rarely travel with the group and commonly spend the whole day up to 20-50m away; this was the group which showed a slight preference for 'gaps' (although this was not significant).

Another theory would be that the size of home ranges increases due to a reduction of food trees and the need to occupy a larger area in order to have a variety of seasonal food and enough feeding sites for the whole group. Although, in a before-and-after logging study by Johns (1985), *H. lar* showed no real change in home range size following the logging, but there were changes in some aspects of their activity budgets: more resting and less feeding and travelling. These alterations perhaps resulted from a decrease in the availability of their favourite, most nutritious food source (Johns 1985). Everything has a knock-on effect and a consequence and, although it seems that some of these theories may be far-fetched, this could be a reality in the long term if disturbance continues in the area.

There is not much sexual dimorphism in agile gibbons, males are reported to weigh on average about 6kg, whilst females, 5.6kg, an average difference of only 7% (Schultz 1973). This is generally expected in monogamous species (Ralls 1977). In contrast, gorillas (*Gorilla gorilla*), which are polygynous, are believed to show one of the highest degrees of sexual dimorphism, with captive males weighing 169kg and females just 80.3kg, a difference of 53% (Leigh and Shea 1996).

Many studies have shown differences in body size and how this can affect certain aspects of behaviour, such as food choice, the presence of infants, morphology and, probably most importantly, social activity (Chatani 2003). In this study, body size was a limiting factor in some aspects of locomotion, but not in others. Females with infants jumped from lower heights and jumped over shorter distances than males. They were generally less willing to take arboreal risks, as would be expected when carrying a dependent infant. A theory for these actions could possibly be the social role of the male, as it is his prerogative to look after the group and, thus, his own genes. Males typically defend the territory and, although the female plays a large part in this, it will generally be the male who gets involved in physical fights. Thus, he must be of greater body size and muscle mass, be able to jump further and be more confident taking-off from higher levels. Nevertheless, females with infants are already constrained in their use of canopy strata and gaps are putting further limitations on the type of canopy they are able, and feel comfortable to use.

The most fundamental part of efficient travel in the forest is the conservation of energy. It is important for the gibbons to take the most direct route of travel available to them, thus preserving energy needed for other activities. Gaps in the canopy pose a problem for this, as they eliminate areas of forest in which gibbons are able to travel, thus forcing them to take less direct, more energy-costly travel routes. As these are an exclusively arboreal species, this poses a major threat to their survival.

Obtaining more knowledge of the forest canopy and the level of disturbance that gibbons can tolerate will help us understand how forests can be managed with gibbons in mind. Under the condition that selective logging of a certain area was to be undertaken, there must already be an understanding as to what level of canopy disturbance the gibbons can tolerate before the population becomes unsustainable (i.e. energy expended in travel becomes too high), but sustainable logging is rarely sustainable. It normally involves the harvesting of rarely more than 10% of trees and leaves the rest to regenerate naturally, although, depending on the techniques of harvest, from between 5 and 70% of all original trees are likely to be destroyed (Johns and Skorupa, 1987). In a study by Cannon *et al.* (1994), after eight years, there was only minimal evidence of canopy regeneration and the density of large, dead trees was greater than that in more recently logged areas (six months to a year), suggesting that they took time to die. Thus, if logging is not immediately destructive, it can have effects that last a long time. If, after over ten years of regeneration, their behaviour is still affected, as I have shown that it is, then this is a rough indicator as to what level of habitat disturbance is tolerable. Depending on the intensity of logging, or selective logging in an area, and the subsequent stage of regeneration, the affects it has on locomotor behaviour will vary. The study site was selectively logged for over ten years, thus the consequences of a longer period of selective or intensive logging will further affect the locomotor behaviours. Speculatively, doubling the time spent logging (over twenty years) would detrimentally change the behaviour of the gibbons and potentially force them to come to the ground to cross gaps or to expend much more energy in an uneven canopy environment than would be necessary in an undisturbed habitat. This study would benefit from a longer study-period for comparison between the before-and-after effects of logging.

One of the main reasons primate populations do not survive well in the presence of logging is the depletion of food sources (Dittus 1977). Chivers (1974) proposed that this is possibly counter-acted in the short term by the increased leaf availability and fruiting from the remainder of trees that are responding to competition from potential new colonisers. Having the capability to modify foraging strategies and increase the diversity of diet, in order to deal with the alterations in habitat and variations in food sources, is probably instrumental for the continued survival of the species in disturbed habitats. In a study of *H. lar,* they became opportunistic feeders, eating a variety of fruit and a higher proportion of leaves following logging (Johns 1985). Gibbons, in comparison with some species of colobus monkeys, are restricted in their capacity to digest leaf material (Vellayan 1981), which may have a negative effect on their energy balances. This concept is supported by Raemaekers (1980), who demonstrated that the amount of certain foods eaten daily corresponds to day-range length.

Since most primate species require a forest habitat in which to live (Wolfheim 1983), and the predicted rate of destruction will leave only fragments of pristine rain-forest by the year 2035 (Johns 1985), the strategies primates use to survive in these areas are of critical importance in devising effective management plans. Gibbons show an incredible degree of flexibility in terms of habitat use, a quality that is rare among other mammals (Johns 1985). Many species are not likely to survive in fragmented habitats and their outlooks are uncertain, but effective management of both national parks and disturbed habitats will strengthen the number of sustainable populations that can be conserved in the future.

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