

Play behaviour and activity budgets of
non-adult, wild southern-Bornean
gibbons (*Hylobates albibarbis*), in the
National Laboratory for Peat-Swamp
Forest, Sabangau Catchment,
Indonesia.

Kate Moise

Oxford Brookes University

September 2009

Word Count: 12,948 words

CIMTROP



Abstract

The study of non-adult gibbons' social behaviour is a new and understudied area of research, we have limited understanding of the dynamics of inter and intra-group social behaviours.

We aimed at quantifying the social and play behaviour displayed by non-adult, wild-southern-Bornean gibbons (*Hylobates albibarbis*); testing differences in age, sex, social partner choice and between group differences. We constructed activity budgets and compared these with adult activity budgets from groups in the same research area.

The gibbons studied were members of three groups of habituated gibbons at the Natural Laboratory Research Area (LAHG), in the Sabangau Forest; consisting of two infants, two juveniles and four sub-adults.

We found marked difference in play behaviour between age groups, with infants exhibiting higher levels of play behaviour than either juveniles or sub-adults; levels of play were higher than expected and markedly higher than that of adults. Differences between groups were small.

The study emphasises the social needs of young gibbons. The findings suggest that non-adult gibbons would benefit from being kept in family groups, when possible. This study will be useful to zoos and rescue centres that care for gibbons, as the findings have implications for the husbandry of captive gibbons and highlight the huge impact taking non-adult wild gibbons away from their familial groups may have on their development and welfare. It also emphasises the distinct gap in knowledge and research that exist about the non-adults of the *hylobatidae* species.

Acknowledgements

I would like to convey my sincere gratitude and appreciation to the field assistants at the Setia Alam Research station, without whom I could not have conducted the research or been able to identify and follow the gibbons as well as I did and would probably still be stuck in a canal in the forest! They were invaluable in their support and dedication to my project, offering guidance and humour to keep me going through the early mornings and days when no gibbons were to be found- Andrea Hoëing, Adul, Aman, Dewa, Santi, Twenti and Yudhi.

I would also like to thank Dr. Susan Cheyne, without whom this project would never have happened. Thank you also for the support, unerring confidence in my ability and the projects worth and for getting me into the forest!

Thank you to my Indonesian sponsor CIMTROP, especially Dr Suwido H. Limin, for supporting my research and providing letters of support for my visa.

This research was made possible by the financial support received from the Chester Zoological/Veterinary studentship.

I would also like to thank the staff at OuTrop for their help, encouragement and support whilst I was in the field: Simon Husson, Helen Morrogh-Bernard, Karen Jeffers, Ibu Yanti, Lis and Mama Agung.

Thanks to my supervisor Dr Vincent Nijman for all his advice and patience in the face of numerous questions and worries.

Finally, special thanks to my family who have supported me through the project and read through numerous drafts, Ryan Covey for advice and proof reading and, finally, thank-you to Fiona Rowe for keeping me relatively sane and providing entertainment and company throughout the write-up.

Table of contents

Title page	
Abstract	i
Acknowledgements	ii
Table of contents	iii
List of tables	v
List of figures	vi
List of abbreviations	vii
Chapter I: Introduction	1
1.1 Play Behaviour	1
1.2 Study Species	7
1.3 Research Questions and Hypotheses	10
Chapter II: Methods	11
2.1 Study Site	11
2.2 Data Collection	11
2.3 Study Species	15
Chapter III: Results	18
3.1 Tree Usage	18
3.2 Activity Budgets and Play Behaviour	20
3.3 Nearest Other Gibbon	24
3.4 Qualitative Data	25
Chapter IV: Discussion	27

4.1 Activity Budgets	27
4.2 Play Behaviour	30
4.3 Tree Heights and Gibbon Height in the Tree	34
4.4 Nearest Other Gibbon	35
4.5 Qualitative Data	36
Chapter V: Conclusion	39
5.1 Future Research	39
5.1.1 Activity budgets	39
5.1.2 Play behaviour	39
5.1.3 Sub-adults	39
5.2 Conservation Implications	40
5.3 Captive Management	40
References	42
Apendices:	51
Appendix I	51
Appendix II	52

List of Tables

Table 1: Ethogram of the behaviours recorded.	14
Table 2: List of the tree height categories.	15
Table 3: List of all the gibbons in the study groups.	17
Table 4: The percentage of social, play and singing behaviour, a comparison between <i>Hylobatidae spp.</i> ,	23

List of Figures

Figure 1: A map of the LAHG	12
Figure 2: A map of the Setia Alam Grid	16
Figure 3: Distribution of tree heights, used by non-adult gibbons.	18
Figure 4: Distribution of non-adult gibbons' height in tree.	19
Figure 5: The percentage of primary behaviours observed in non-adult gibbons.	20
Figure 6: The percentage of primary behaviours of adult and non-adult gibbons.	21
Figure 7: The percentage of primary activities for infant gibbons.	21
Figure 8: The percentage of secondary play behaviours for non-adult gibbons.	24
Figure 9: The nearest other gibbon percentage for non-adult gibbons.	25

List of Abbreviations

CIMTROP	Centre for the International Management of Tropical Peatlands
CITES	Convention on the International Trade in Endangered Species
IUCN	International Union for the Conservation of Nature
LAHG	Laboratorium Alam Hutan Gambut (natural laboratory for the study of peat-swamp forest)
OuTrop	Orang-Utan Tropical peatland and conservation project

Chapter I: Introduction

Play Behaviour

The occurrence of play behaviour has been discussed exhaustively (Fagen, 1974; Hinde, 1975; Bekoff and Byers, 1981). It has been argued that play behaviour does not exist; that it is unimportant because it is the first behaviour to be dropped when an animal experiences pressure or stress, and that it is not present in all mammals (Fagen, 1981). Though it is now out-dated to believe that play does not exist it is still often not the focus of many activity studies as it constitutes such a small proportion of many animals' daily activity budgets, this is especially true of adult animals. However, it is argued that play behaviour is of vital importance to the development of young animals (Lee, 1984). Play is witnessed in most mammals (Bekoff, 2001) from as early as a few weeks old. "Play with peers is one of the first non-mother-directed behaviours to appear early in life" (Bekoff, 1972). Biben (1998) found that infant squirrel monkeys (*Saimiri sciureus*) reached out to each other at as young as five weeks of age, whilst still being carried on their mother's backs. Primates are excellent candidates for the study of play as they have extended immature periods compared to most mammals (Joffe, 1997) and, therefore, have a longer developmental period than most, highlighting the importance of this age. The small amount of time assigned to play behaviours is not reflective of the importance play has for non-adult animals.

Bekoff (1972; 2001) says that play is imperative to a juveniles development of acceptable behaviour and boundaries and that the absence of play can affect the development of social behaviours. The importance of social interaction is of importance to rehabilitation centres and zoos as well as understanding affiliative behaviour in the wild. Harlow and Harlow *et al.* (1965, 1965) conducted a series of seminal studies highlighting the importance of early social experiences on rhesus macaques (*Macaca mulatta*). These authors found that maternal deprivation adversely affected social development; this was also true when infants were deprived of conspecific interaction as well. They found that natural aggressive reactions became self-directed and abnormal in their occurrences and strength of response. They also found that sexual behaviour did not develop either at all or if it did it was inadequate and did not result in pregnancy. Though these are all social behaviours and not just

play, it highlights the importance of the ability to interact with other conspecifics on the development of appropriate behaviour. Hol *et al.* (1999) found there is a sensitive period in development; using rats (*Rattus norvegicus*) they found reduced social activity, when the rats were re-housed with conspecifics, after being housed in isolation during the sensitive period. The sensitive period was between four and five weeks of age. It is likely that this is a lot longer in primates as they have extended juvenile periods (Joffe, 1997). Sensitive or critical periods of development are displayed in many mammals; in domestic animals it is often referred to as the socialisation period. It is thought that if an animal does not encounter something in this period of time they will be more fearful of it later in life (Freedman *et al.*, 1961; Appleby *et al.*, 2002). The ability to interact with others of the same species is of utmost importance to group living social animals; if they cannot form bonds and live with other animals they will not be able to form groups and benefit from the positives of group living. This is just as true of family living gibbons as it is of primates that live in larger groups. Gibbons pair bond with a partner and live with them and consequent offspring. These pair-bonds are imperative as, if a gibbon does not manage to secure a pair bond with another gibbon, they may have a higher chance of being predated, or attacked by another group; as studies show that the benefits of group living, protection for example, outweigh the costs, resource competition (Rubenstein, 1978; Van Schaik and Kappeler, 2003). Cheyne (2004, 2009c, in press) have highlighted problems associated with gibbons raised in captivity; documenting abnormal behaviours, “developmentally stunted social behaviours” and “under developed social skills” (Cheyne, in press). These findings compound the idea that young animals social needs must be met for their full development potential to be reached.

The developmental effects of play and social activities on the brain have been shown to be fundamental. Byers and Walker (1995) discuss the magnitude of play behaviour on the development of cerebellar synaptogenesis and muscle fibre differentiation. They state that purkinje synapses, retention and ultimate number of, are experience-dependant. The sensitive period for the development of these synapses occurs at the time that play behaviour is most prevalent. This is not surprising as juveniles brains are developing rapidly and new pathways are constantly being created, these pathways must be used often to be retained. As with the critical period, it is important

that young animals encounter as many different situations as possible. Young animals are highly explorative, with play in infants being focused on this. This focus changes as they get older, coinciding with the brain pathways being less flexible (Baldwin and Baldwin; 1974; Hol, 1999). The importance of play on brain development emphasises the implications if non-adult gibbons are not provided with the opportunity to play.

Spinka *et al.* (2001), state that play allows young animals' to prepare for unexpected events. This will be of obvious importance to gibbons as they move quickly through the trees and have to adapt quickly to changes in surroundings and environment. They also suggest that this practice allows animals to cope with stressful events more easily. Unexpected events occur frequently in a wild animals' everyday life; for gibbons these events could range from a branch giving way, when they use it in travel, or coming into contact with a predator. The knowledge of how to orientate themselves, kinaesthetic awareness of their bodies and actions and pre-practised movements in safe environments will all be imperative when they have to make split second reactions or decisions to situations. Play involves lots of motor movement and, especially for arboreal animals, will involve being inverted at different angles and ways. Spinka *et al.* (2001) suggest that with practice speed, agility and recovery after a fall or collision will be increased and more successful; these types of behaviours occur frequently during auto and partner orientated play. Using the example of an animal fleeing from danger, they say that the animal may be "disorientated... [and] the ability to recover rapidly using atypical movements could mean the difference between life and death in a predator attack" (p.143). Lewis (2000, p.420) states "social play interactions require a greater level of social cognitive ability..." This cognitive ability can only be developed with the correct exposure to social interaction when the animal is young (Harlow, 1965). Play is also thought to prepare young animals for future behaviours. Play fighting and chasing can help prepare the animal, as the skills involved in play mirror those used in actions which could be imperative to their survival.

Boulton and Smith (1992) discuss the costs and benefits that are involved in playing with a conspecific. If it is true to say that the player gains something from the act, experience for example, then it could also be true that the other player may have to

make a compromise. They use the example of wrestling where the players appear to take turns at being the “dominant” player, the dominant position will allow the player to practice their skills; whereas the non-dominant player will possibly have to inhibit their strength and skills and may not get as much of a reward out of the play as the other. They suggest that the reasoning behind this could be reciprocal altruism, if they facilitate play with a conspecific they will play with them back and will allow role reversal as well. This idea has led to similar theories involving a concept called self handicapping (Bekoff, 1984; Pereira and Preisser, 1998; Spinka *et al.*, 2001). Spinka *et al.* (2001) put forward the idea of self handicapping; which involves the animal creating situations where they cannot function fully and involves more concentration or different movement to complete a task. “The deliberate attenuation of the force or intention of an action by one or the other play partners in order to give the other a better chance of ‘winning’...” (Boulton and Smith, 1992, p. 436). It could also involve an animal “inhibit[ing] the force of their bite,” (Spinka *et al.*, p.144) for example, thus allowing play to continue and meaning the smaller, weaker playmate will keep playing with them and not avoid them. This sometimes will result in the younger one taking it too far and the older animal having to “reprimand” them, this helps the younger animal learn about dominance and the ‘rules’ of play. Self handicapping has also been documented in human children (Aldis, 1975; Fry, 1987), suggesting the evolutionary importance of the handicapping theory. Self handicapping may occur in gibbon juvenile play as, because of the dynamics of a gibbon group, young gibbons with quite large age differences may be play partners. The difference in ages is due to the large inter-birth intervals that are characteristic of gibbons (Mitani, 1990; Cheyne and Brulé, 2004, Cheyne, in press). Gittins and Raemaekers (1980, p. 72) state that “if play occurs [in non-adult gibbons], it must either be solitary or with an individual at least two years older or younger.” The difference in age is centre point to the belief of low amounts of play behaviour occurring.

The other vital aspect of play behaviour concerns the mental well-being of the animal; this has been acknowledged since the mid-1800’s (Darwin, 1874; Bekoff, 2001). “Happiness is never better exhibited than by young animals, such as puppies, kittens, lambs, etc., when playing together, like our own children” (Darwin, 1874, pp. 70). The importance of an animal’s mental well-being should never be underestimated or

forgotten. The examination of play behaviour has important implications for the management and husbandry of animals in captivity. The needs of animals in captivity, social, physical and mental can be gauged using information gathered from *in situ* studies. A study by Cheyne (2007d) shows there is a number of abnormal behaviours displayed by captive gibbons that are not present in wild gibbon populations. Cheyne suggests these are due in part to inadequate opportunities for social interactions. Mallapur and Choudhury (2003) also suggest some abnormal behaviours may be due to early social deprivation, usually in the first year of life; though they also suggest that inappropriate foraging opportunities will affect some abnormal behaviours.

The benefits that play behaviours appear to provide are diverse, but a definitive benefit has not been agreed upon. This could be because the benefits are numerous and differ depending on species and age or sex for example. It is often delayed benefits that are thought to be of most importance and the immediate benefits are overlooked. The delayed benefits include motor training, decision making and behaviour acquisition (Martin and Caro, 1985; Caro, 1995; Suomi, 1997; Bekoff, 2001). The immediate benefits may include a positive internal feedback system, meaning that play elicits a positive feeling so the behaviour is repeated. Play also helps to unite a group and strengthens bonds between siblings, parents and offspring. The importance of social cohesion is accepted and understood, social acts like play, and grooming often facilitate this. The implications that play behaviour has on an animal's development could be far reaching and form the basis of integral behaviour components.

While play behaviour has been documented in a range of animals, including humans and many species of primates (Fagen, 1974, 1981; DiPietro, 1981; Martin and Caro, 1985); gibbons have been understudied in this area, due to the difficulty of observing these behaviours *in situ*. The relatively small group size, gaps between births and speed of gibbons poses difficulties for observers. It was also originally thought that gibbons performed incredibly low amounts of social behaviours (Ellefson, 1974); although this has now been refuted (Bartlett, 2003; Cheyne, 2004, in press) it has never been studied in non-adults, so a true representation of play behaviour cannot be given.

Defining play behaviour is one of the problems to be encountered when discussing and researching such behaviours, though Martin and Caro (1985) and Bekoff and Byers (1981) attempt to define play by detailing it as a behaviour that does not appear to have obvious function or immediate benefits. However, defining play is problematic as it is not fixed, there are many components and it can happen in a variety of circumstances. It might also be assumed that there are signals and cues being employed that are not always obvious to the observer. To engage in play both parties must acknowledge that this is not a serious encounter; for example, that the chasing will not end in being caught and harmed, though wrestling may ensue (Bekoff, 1972). For this to happen there must be cues, subtle and unsubtle that can be interpreted by the players. Biben (1998) found that, especially when monkeys are a few months old, mothers intervene less and less during play, demonstrating that they too can read the play signals and meta-communication and can see that it is not serious. It is harder for researchers to identify the beginning and end of play and to determine the initiators, so for play to be studied effectively a descriptive ethogram will be needed. These problems mean that comparison between species is very difficult as play seems to be displayed differently and costs and benefits also vary between species, age and sex (Bekoff, 2001). For this study it is accepted that play behaviour does occur, but the effects of play behaviour and costs and benefits involved are open to more debate and further examination.

The importance of play behaviour is often discussed and criticised. Behaviour studies are often considered entirely separate from conservation studies and vice-versa (Sutherland, 1998). Mittermeier and Cheney (1987, p.496) state that providing knowledge about the behaviour of understudied and endangered animals is “critical to conservation efforts.” The importance of research into behaviour and activity patterns must not be underestimated, for help can not be given if the species is not understood. Knowledge about group activity patterns, habitat and substrate use and social interactions are imperative for the conservation of a species. Without this knowledge it is impossible to design and implement ways of conserving the habitat and to recognise changes occurring due to ecological pressures. Play behaviour can be considered a frivolous activity; but the importance of play behaviour in an animals’ development cannot be overlooked. It was previously thought gibbons displayed little

or no social behaviour. Ellefson (1974), states that “gibbons have generally been perceived as engaging in very low rates of affiliative social behaviour relative to other primates.” Leighton (1987) conducted a study showing that socialising made up an unexpectedly small amount of gibbons activity budgets. It has been suggested that these findings may be due to the difference in social structure and group size in gibbon groups, when compared to other primates, as gibbons live in small familial groups (Chivers, 1977) and have large inter-birth intervals. Due to the age difference in offspring there was thought to be little opportunity for social behaviour between younger gibbons. Bartlett (2003) puts forward the idea that gibbon social behaviour may be better compared to ateline species, as they are more arboreal species and have similar group sizes. It must also be acknowledged that the majority of studies conducted on gibbons and their social behaviour are focused on adults; as play is demonstrated at much higher levels in non-adults it would seem more prudent to investigate them. However, recent studies have shown that higher rates of social interactions occur than previously thought and that this is also true of between group interactions; (Bartlett, 2003; Cheyne, 2004, in press) showing that this is an area that needs more attention.

Study Species

Gibbons are small, socially monogamous apes and are generally difficult to study because they are fast moving and arboreal (Chivers, 1977; Cheyne, in press). There is some debate over the classification of gibbon species; but it is thought that there are at least twelve separate species (Brandon-Jones *et al.*, 2004). Gibbons are mostly frugivorous animals, but supplement their diet with flower buds, leaf shoots and invertebrates (Gittins and Raemakers, 1980; Cheyne, 2008b). Gibbons live in small familial groups, consisting of up to five animals, including two parents, and possibly one or two sub-adults, a juvenile and infant. Gibbons have large inter-birth intervals, studies show that across species there can range from twenty-two months between births to one hundred and twenty months (Chivers and Raemaekers, 1980; Reichard and Barelli, 2008). This difference in age, of the non-adults in a group, means that play behaviour will have to occur between different aged and therefore sized siblings. For even if, as Bartlett (2003) states, inter-group encounters result in play for similar

aged gibbons, these encounters are likely to be short and infrequent; owing to the territoriality of the adults in the group. There is little sexual dimorphism between adult gibbons and this had led to the belief that neither sex is dominant (Gittins and Raemaeker, 1980). Gibbons are also highly territorial, it is well documented that they will defend their territories and it is thought that part of the reason that gibbons sing is to defend their territory, as well as to strengthen pair bonds (Mitani, 1987a; Cowlshaw, 1992). The calls are distinctive, “the most easily recognisable one being the female’s great call” (Cheyne, in press), and differ between species and sex (Geissmann and Orgeldinger, 2000; Cheyne *et al.*, 2007a). Gibbons are thought to be socially monogamous and to pair for life (Gittins and Raemaekers, 1980). Adult gibbon pairs are highly tolerant of each other, “aggressive interactions are infrequent” (Gittins and Raemaekers, 1980, p.71). However, recent studies have suggested that extra-pair copulations may occur (Palombit, 1994a, 1994b; Sommer and Reichard, 2000; Bartlett, 2001). The occurrence of extra-pair copulations could have an effect on the behaviour of the adult males towards the young, though this is unlikely as in extra-pair copulations there is usually a chance that the paired partner could be the parent, meaning that parental investment is still ensured (Birkhead and Møller, 1995). It is possible there could be an effect on inter-group dynamics, if extra-pair copulations are occurring. There are large differences in gibbon densities across study sites but these differences have yet to be fully explained (Leighton, 1987; Cheyne *et al.*, 2007; Cheyne, in press); showing that a more in depth knowledge of these under-studied apes is needed, to help provide appropriate protection for their habitats and, therefore, them.

Knowledge about gibbons’ activity budgets is important because the proportion of time that animals spend in different activities and the distribution of these activities throughout the active period is of great importance for species ecology. Activity profiles allow us to understand how a species uses resources and adapts to its environment. It has been found that adult gibbons in the LAHG have an average activity budget of “29% resting, 29% feeding, 29% travelling, 9% singing and 4% in social activities” (Cheyne, in press). Adult gibbons’ activity budgets have been documented (Raemakers, 1979; Gittins, 1982; Cheyne, in press), but little is known about the non-adult individuals, this study hopes to address this fact. This study aims

to assess group dynamics and gain a greater understanding of the cohesion and behavioural relationships within gibbon families.

Gibbons, like all primates, face external threats from humans, including the destruction of their habitat. Peat-swamp forests are subjected to logging, concessionary and illegal, like other forests across the world. The National Laboratory for Peat-Swamp Forest, Sabangau Catchment (LAHG), was originally a logging concession and after the Indonesian economic crisis in 1997-1998 illegal logging occurred (Nijman, 2005; Morrogh-Bernard *et al.* 2003; Cheyne, in press). The logging has transformed the forest into degraded secondary forest; this will not only affect the heights of available trees in which the gibbons can travel, but also alter feeding and normal behavioural patterns, as the trees are smaller than in pristine forest. The pet trade also has a large impact on gibbon populations and possibly on their behaviour as well. The illegal pet trade in Indonesia is a problem that affects a large range of animals. Nijman (2005), shows that although the impact of direct trade on the gibbon population of Borneo is relatively small, the indirect consequences are extensive. For every gibbon that ends up as part of the pet trade at least one more was probably killed, as the mothers of infants are shot. The effects of this practice are large and far-reaching. The obvious consequences are that the infant will end up as a pet, or at best in a rescue centre, and the mother is killed. However, the removal of two members of a familial group is likely to have a huge impact on the remaining family members.

Geissmann (2007) suggests that gibbon populations will decline due to the rapid rates of destruction peat swamp forests are subjected to. Peat swamp forests in the Indo-Malayan regions are predominantly located in Kalimantan and Sumatra (Page *et al.* 1999; Page, 2002). Historically peat swamp forests were of little interest to conservationists as they were thought to have low biodiversity; they also contain numerous species of trees that are of high commercial use and were, therefore, not protected (Reiley *et al.* 1997; Page *et al.*, 1999b; Morrogh-Bernard *et al.* 2003). Due to the commercial interest in the tree species within peat swamp forests and the assumed lack of biodiversity, they have been extensively cleared and cultivated. However, recent studies have shown that despite the highly acidic, nutrient poor soil

and the annual flooding, peat swamp forests have tree species diversity comparable with forests that are mineral soil based (Rieley *et al.*, 1997; Felton *et al.*, 2003).

The focus of this study is the southern-Bornean gibbon (*Hylobates albibarbis*). These apes were originally thought to be a sub-species of *Hylobates agilis*; but have since been recognised as a species in their own right on the recommendation of the 2006 Asian Primate Redlist Workshop (Geissmann 2007; Cheyne, in press). *Hylobates albibarbis* are endemic to Borneo and found between the Kapuas and Barito rivers (Brandon-Jones *et al.*, 2004; Cheyne, in press). *Hylobates albibarbis* are listed as endangered on the IUCN Redlist (Nijman *et al.*, 2008) and are CITES I appendix listed, meaning commercial trade is prohibited (UNEP-WCMC, 2009).

Research Questions and Hypotheses

Previous research on non-adult gibbons is scarce. The paucity of this knowledge is the focus of this study. The first aim is to gain knowledge about the behaviour of non-adult gibbons, constructing activity budgets of their primary behaviours. The second aim is to ascertain whether play behaviour occurs and what sort of form these behaviours take if they do happen. Using knowledge from previous play behaviour studies, in other primate species, an ethogram will be formed and used to distinguish the behaviours.

The hypotheses are:

Non-adult gibbon activity budgets will be similar to adult activity budgets of the same species.

Play behaviour will be present.

Play behaviour will decrease with age.

Differences between group activity budgets and play behaviour may differ depending on the structure of the groups.

Nearest other gibbon will show a difference between age groups.

Chapter II: Methods

Study Site

The National Laboratory for Peat-Swamp Forest, Sabangau Catchment (LAHG), managed by the Centre for the International Co-operation and Management in Tropical Peatlands (CIMTROP, University of Palangka Raya) is located in the South of Borneo in the region of Kalimantan. The Setia Alam Field Station is 20 km southwest of Palangka Raya in the upper reaches of the Sabangau River (Figure 1.). The region of Kalimantan has peatlands covering about six million hectares of the lowlands (Rieley *et al.* 1997). The Sabangau catchment covers an area of approximately 5300 km² and is sited just inside the forest edge on a former logging concession (Figure 1) (Cheyne, 2008b). Conversion and unsustainable logging threaten the forests of Borneo; the peat-swamp forest of the Sabangau also faces the threat of burning due to El Niño. The LAHG “was gazetted as a national park in November 2004, after having been allocated to logging companies for timber extraction for thirty years” (Cheyne, 2009b). Due to “the high density and volume of commercial timber in Kalimantan, intensively logged forests typically have 80% of the canopy basal area removed or destroyed” (Curran *et al.*, 2004). The effects of logging are far reaching, affecting the eco-system through loss of trees and the infra-structures put in place; for example, the canals dug to transport felled trees drain the peat and leave it more susceptible to fire. Fire is one of the major threats to peat-swamp forest and, therefore, the gibbons that live there. The burning of a peat-swamp forest has huge implications as it is a massive source of carbon, if the peat burns this is released into the atmosphere. Page *et al.* (2002, p. 61) extrapolated the effects of forest burning in Borneo and found that the carbon emission was “equivalent to 13–40% of the mean annual global carbon emissions from fossil fuels, and contributed greatly to the largest annual increase in atmospheric CO₂ concentration detected since records began in 1957”. The fires that occur in Kalimantan are sometimes man-made and sometimes natural; happening due to lightning, for example. The main problem is that once the fires start they are nearly impossible to control. Patrol teams do exist, there is a team at the LAHG, but they are underfunded and cannot protect the whole of the Sabangau (Cheyne, 2009b). The area has been the focus of regeneration (Page *et al.*, 1999b), hydration, ecological and animal behavioural studies (Morrogh-Bernard H, 2003; Morrogh-Bernard H, *et al.*, 2003; Cheyne *et al.*, 2008). Peat-swamp

forest is one of the major components of the southern-Bornean gibbons' habitat, a very small proportion of which is protected within national parks (Morrogh-Bernard, 2003; Haag, 2007; Cheyne, 2008b). It has been found that the Sabangau is home to the largest remaining wild population of Bornean orang-utans (*Pongo pygmaeus*) (Morrogh-Bernard *et al.*, 2003) and a large wild population of southern-Bornean gibbons (*Hylobates albibarbis*) (Buckley *et al.*, 2006; Cheyne *et al.*, 2007b; Cheyne, in press).

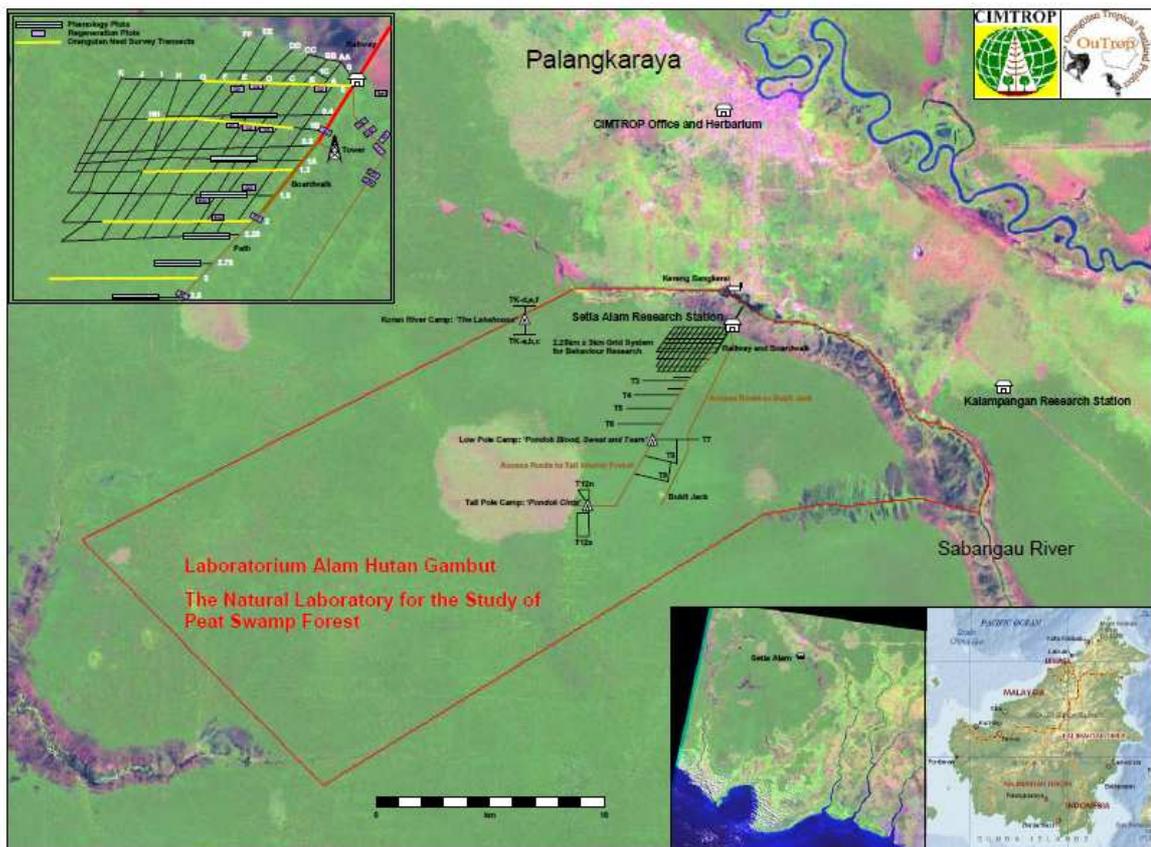


Figure 1. A map of the LAHG, with the Setia Alam grid in the left hand top corner. Where the LAHG is in Borneo is detailed in the bottom right corner.

Data Collection

This study was carried out from 13th May-27th July 2009. For this study, each group was followed for three days in a row. The focal was rotated so that all focal gibbons were followed for at least thirteen hours and following was spread evenly, for all focals, over the three months. Gibbons were found using their morning songs to locate the group or, if they did not sing, by searching their territories, which are

known and documented (Cheyne in press) (Figure 2.). Once gibbons began to sing, researchers approached to a close distance without disturbing the gibbons. Gibbons use morning duetting to defend their territory and to strengthen pair bonding (Mitani, 1987a; Cowlshaw, 1992; Geissmann and Orgeldinger, 2000; Cheyne *et al.*, 2007a). The songs and great calls, “which can be heard up to one kilometre away in flat, dense rainforest, can be used for auditory sampling method in surveys” (Brockelman and Ali, 1987; Nijman and Menken 2005; Cheyne *et al.* 2008) The behaviours being documented in this study were written into an ethogram, including primary and secondary activities (Table 1.). The social and play behaviours have secondary activities as this was the focus of the study and a more detailed description of the behaviours was of interest. A focal animal was chosen and five minute scan sampling was used to record the behaviours. (Altman, 1974; Martin and Bateson, 2007) This method was in keeping with the behaviour sampling methods that were already being used at the site, as this project will be used in comparison with previous and ongoing research. The estimated height of where the gibbon was in the tree and the height of the tree was recorded, using categories that correspond with ones already being used at the study site (Table 2.); the nearest other gibbon and, for the infants, whether they were clinging to the mother or not were also recorded. Estimating the tree heights was practiced and tested until proficiency was achieved, inter-observer bias was avoided by all observers receiving the same training and a thorough discussion of the behaviours in the ethogram occurred before data collection began. The nearest other gibbon involved recording the gibbon that the focal was closest to, when possible, within twenty metres, if no gibbon was within twenty metres they were considered on their own. The data sheets used can be seen in Appendix 1.

Table 1. An ethogram of the behaviours recorded when observing non-adult gibbons (*H. albibarbis*), in the LAHG.

Code	Primary Activity	Code	Secondary activity
F	Feeding		
R	Resting, no or little movement		
T	Travelling, brachiating, jumping or moving with purpose		
C	Calling	Ac	Alarm call
		S	Singing with family
		Cr	Crying
S	Social	Ma	Mating
		G	Groom
		Alg	Allogroom
		Fi	Fighting
P	Play	Mo	movement around tree (no obvious function, not moving to feed or travelling)
		Gr	grabbing/pulling
		Ha	Hanging by arm/s or leg/s on branch or other gibbon
		Cha	Chasing another gibbon
		Ap	Auto play- playing on own with part of focal animals body
		Pb	Play with branch (object)
		Wr	Wrestling, manipulating another gibbon
Wo	Watching observer		
O	Other		
L	Lost		
N	Nursing		
cl/mo	Clinging to mother	m/t	Mother travelling
		m/f	Mother feeding
		m/r	Mother resting
U	Unable to see		

Table 2. A list of the tree height categories used for the study, these categories were also used to document the height of the gibbon in the tree.

Tree height and height of gibbon in tree categories
0_5
6_10
11_15
16_20
21_25
26_30
31_35
36_40

Study Species

The animals in this study were comprised of three separate family groups of wild southern-Bornean gibbons (*Hylobates albibarbis*). The three groups were chosen because they are the most habituated of the groups in the Sabangau and, therefore, are more reliable to follow and collect detailed behavioural data on. The territories of the gibbons and where they are in relation to each other and on the Setia Alam grid can be seen in Figure 2. The family dynamics can be seen in Table 3. There are two infants of different sex, two juvenile males, three sub-adult females and one sub-adult male. The infants were born within two months of each other; the ages of the other gibbons are unknown though they are estimated to be between 5-8 years old. Each group followed is comprised differently so inter-group differences can be looked at and some sex differences can also be assessed.

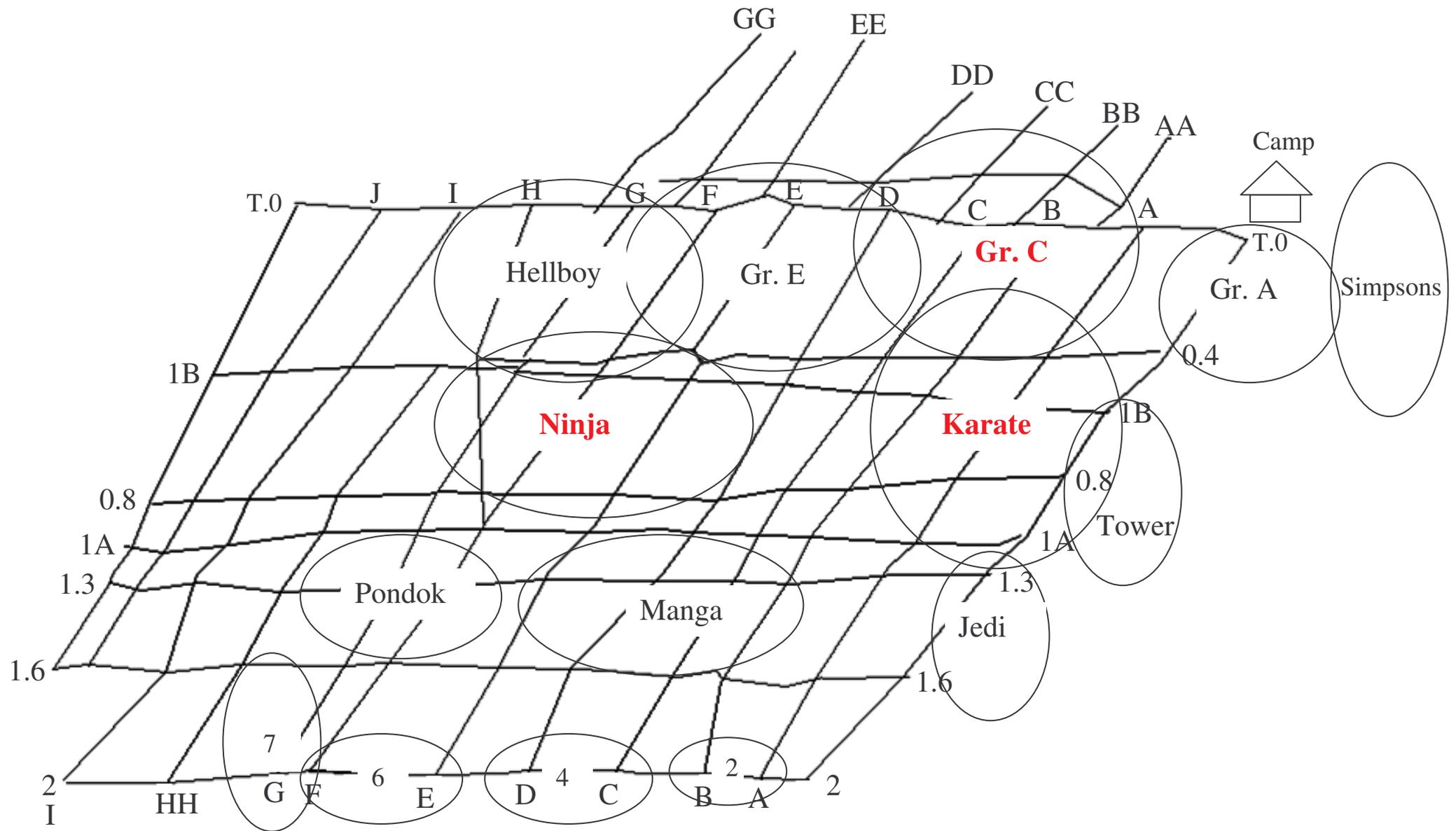


Figure 2. A map of the Setia Alam grid, with the focal groups of gibbons (*H. albibarbis*) for this study highlighted in red.

Table 3. A list of all the gibbons in the study groups

Group	Age class	Name	Focal
Group C			
	Adult Male	Captain Kalaweit	
	Adult Female	Coklat	
	Sub-adult Female	Cynthia	Focal
	Juvenile Male	Coklat	Focal
Karate			
	Adult Male	Bruce Lee	
	Adult Female	Chun Li	
	Sub-adult Female	Zyang Zizi	Focal
	Juvenile Male	Jet Li	Focal
	Infant Female	Brandon Lee	Focal
Ninja			
	Adult Male	Ninja Boss	
	Adult Female	Nikmat	
	Sub-adult Female	Nina	Focal
	Sub-adult Male	Neo	Focal
	Infant Male	Nidji	Focal

This study will look at activity budgets of the three age categories and compare these with findings of adult activity budgets in the same forest. Sex differences and between and within group comparisons will be analysed. For the play behaviour, sex and age differences will be analysed and between and within-group variance looked at. Height of tree and the gibbon height in the tree at time of sampling will be assessed, as will pair associations, as the nearest other gibbon is recorded.

Chapter III: Results

Tree Usage

The three age groups (infants, juveniles and sub-adults) were observed to use trees of different heights unequally ($\chi^2 = 44.84$, $df = 8$, $P < 0.01$); sub-adults were observed disproportionately in the taller trees (26m and above) ($\chi^2 = 6.09$, $df = 1$, $P < 0.05$). Juveniles and especially the infants were observed significantly more in trees of 16-20m ($\chi^2 = 32.56$, $df = 4$, $P < 0.001$) and infants were observed significantly less in trees <16m ($\chi^2 = 16.43$, $df = 2$, $P < 0.001$) (Figure 3). The observations were adjusted to equal proportions.

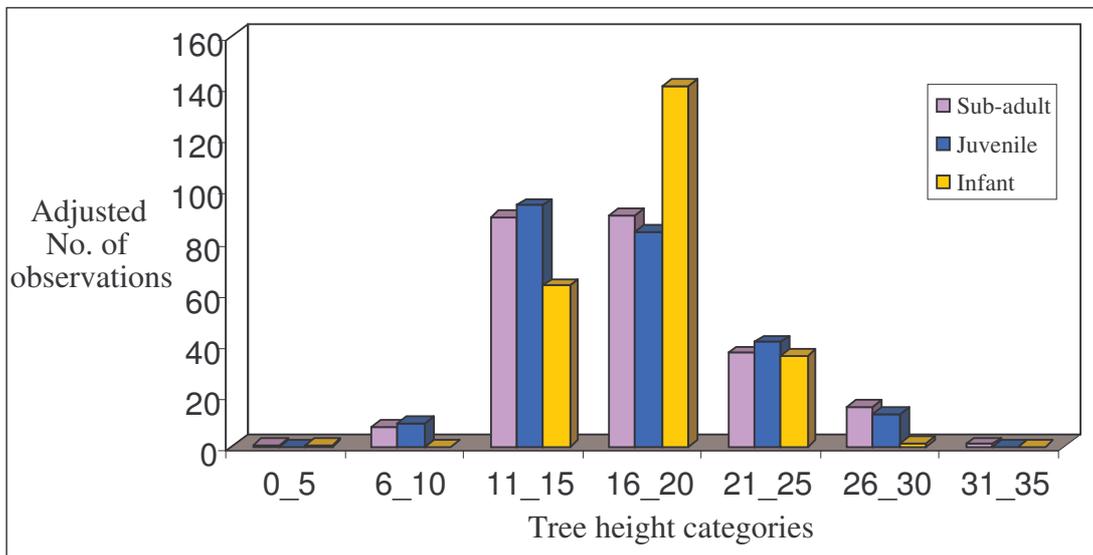


Figure 3. Distribution of trees used by infant, juvenile and sub-adult gibbons (*H. albibarbis*), in the LAHG; showing that infants frequently use trees of intermediate height and sub-adults and juveniles are more evenly distributed.

The trees used whilst play behaviour occurred were then analysed, between age groups, $\chi^2 = 3.58$, at $df = 4$, $P > 0.05$. These findings show the general distribution of play in the different heights of trees was similar to the expected and were not significant for juveniles, infants or sub-adults, though a trend did seem to be occurring for the sub-adults using taller trees slightly more than expected.

Comparing all three age groups, the height of the gibbons in the trees was found to not be evenly distributed ($\chi^2 = 63.95$, $df = 8$, $P < 0.001$) (Figure 4). This was then further analysed to see where the differences occurred. It was found that juveniles

used the trees as expected, but infants and sub-adults did not. When trees > 21m were analysed, sub-adults were found to use these heights significantly more than expected ($\chi^2 = 9.61$, $df = 1$, $P < 0.01$). Compared to other age groups, sub-adults used tree heights >20m significantly more than trees at lower levels ($\chi^2 = 9.6$, $df = 1$, $P < 0.01$).

Infants used the top two canopy levels less than expected ($\chi^2 = 10.58$, $df = 1$, $p < 0.01$). Trees <10m were used significantly less than expected by infants ($\chi^2 = 15.41$, $df = 1$, $P < 0.01$), but middle heights, 16-20m, significantly more than expected ($\chi^2 = 40.95$, $df = 2$, $P < 0.01$).

Between group differences were also examined and significant differences were found when looking at the height of the gibbons in the trees during play ($\chi^2 = 12.28$, $df = 4$, $P < 0.05$). When Group Ninja were compared to the other two groups it was found they used trees >21m heights less than would be expected ($\chi^2 = 6.48$, $df = 1$, $P < 0.05$). It was found that Group C used trees <15m in height significantly less than would be expected ($\chi^2 = 4.50$, $df = 1$, $P < 0.05$).

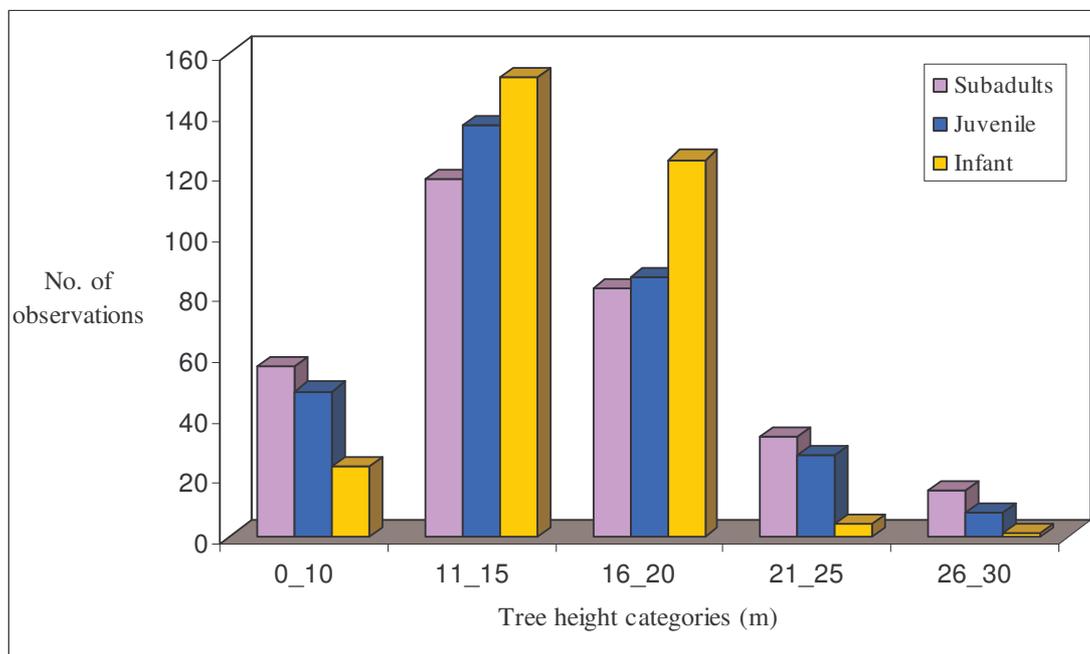


Figure 4. Distribution of infant, juvenile and sub-adult gibbons' (*H. albibarbis*) height in tree, in the LAHG; showing that infants are frequently observed in the intermediate heights whilst juveniles and sub-adults are more evenly distributed, though also with more intermediate height usage.

Activity Budgets and Play Behaviour

Activity budgets for non-adult gibbons were formulated using the primary behaviours. Figure 5 shows that infants display a high percentage of play behaviour when compared to sub-adults and juveniles. Clinging to mother was omitted to allow for direct comparison with sub-adults and juveniles.

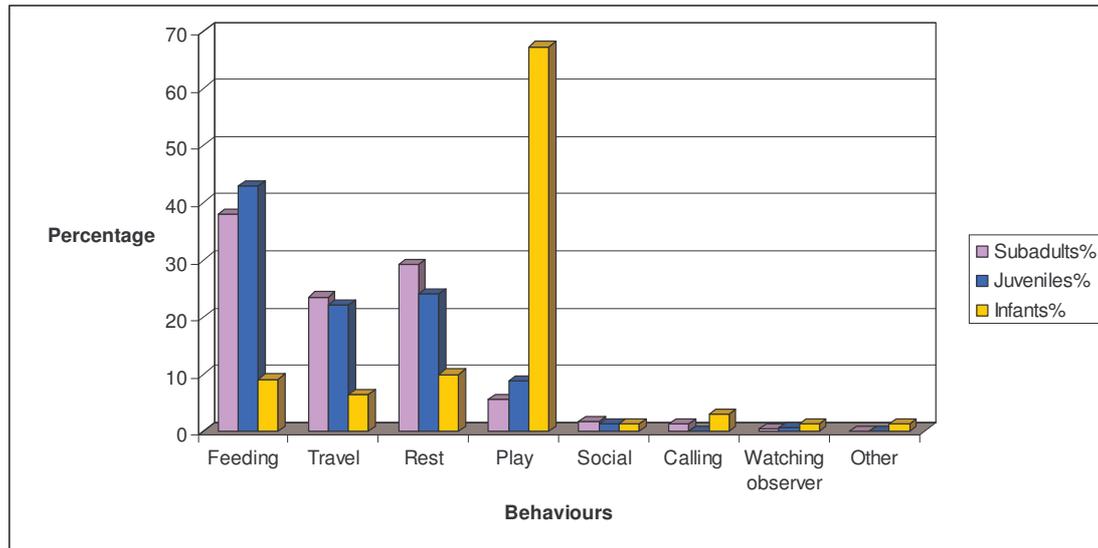


Figure 5. The percentage of primary behaviours observed in sub-adult, juvenile and infant gibbons (*H. albibarbis*), in the LAHG; showing that play accounts for a high percentage of the infants time (clinging to mother has been omitted from this data)

In Figure 6 it can be seen that, when compared to non-adults, adults' behaviour is more evenly distributed between the three categories of feeding, travelling and resting, and they show much less social behaviour than infants but similar amounts to sub-adults and juveniles. Figure 6 shows sub-adult behaviour to be more similar to adult behaviour than the other two non-adult age categories. Juveniles are more similar to sub-adults than they are infants, but not as close to adults as the sub-adults.

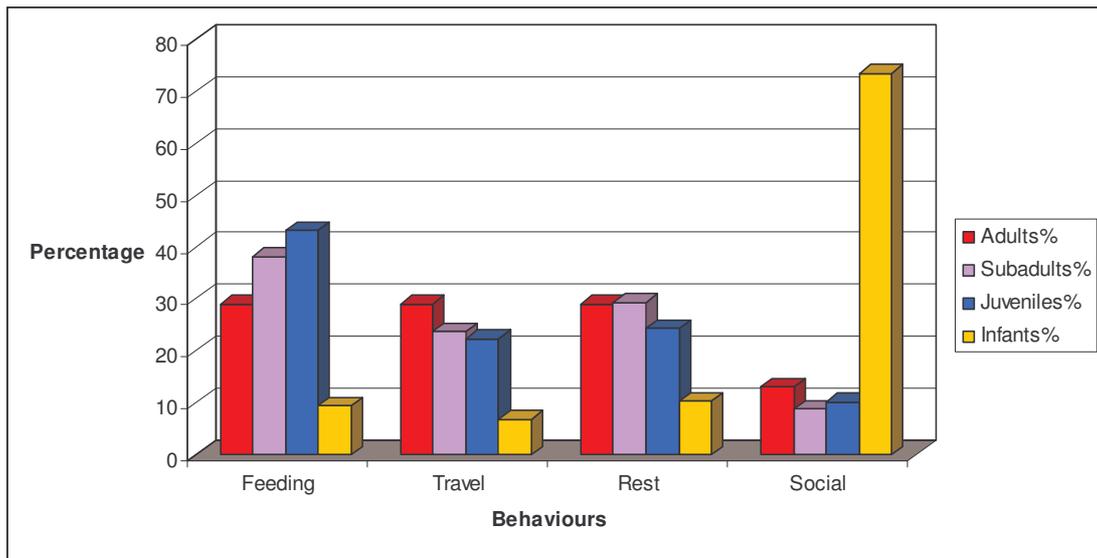


Figure 6. The percentage of primary behaviours of adult and non-adult gibbons (*H. albibarbis*), in the LAHG; showing that sub-adult behaviour is most similar to adult behaviour. The adult activity budgets were obtained from Cheyne, in press.

Figure 7 shows infants participate in play behaviour more than all other behaviours except for clinging to mother. It also shows that infants do travel and feed by themselves.

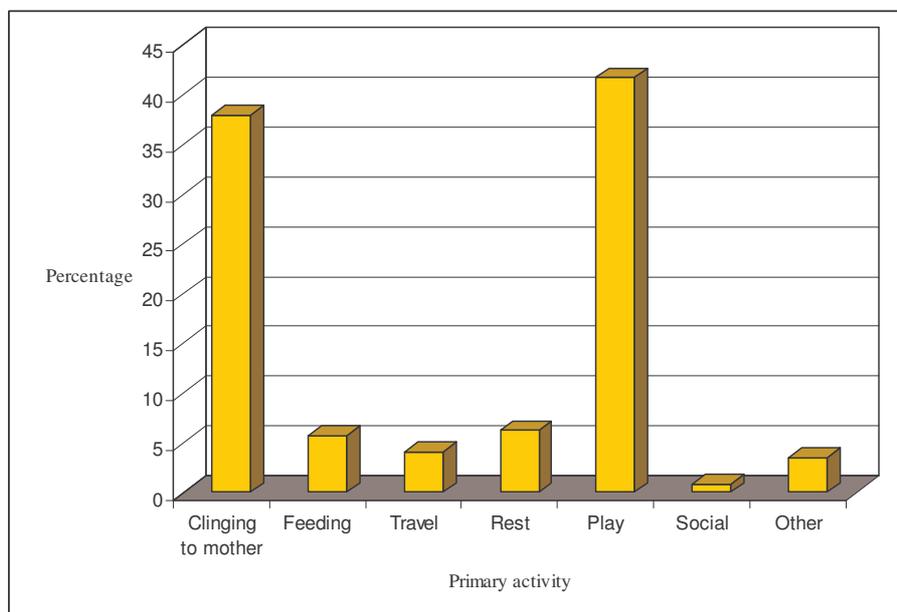


Figure 7. The percentage of primary activities for infant gibbons (*H. albibarbis*), in the LAHG; showing that play is second only to clinging to mother in percentage of activity.

The primary behaviour distributions were analysed within and between age classes, clinging to mother was omitted from the infants results so that a direct comparison could occur. The infants were found to have significantly different behavioural distribution ($U = 44506$, $n^1 = 312$, $n^2 = 321$, $P < 0.01$ two tailed). Juveniles were found to not be significantly different from each other ($U = 11178.5$, $n^1 = 135$, $n^2 = 173$, $P > 0.1$). The sub-adults primary behaviour distributions were not significantly different from each other ($H = 3.84$, $df = 3$, $P > 0.1$)

All three age groups were then compared, showing a highly significant difference in the distribution of behaviour displayed ($H = 255.64$, $df = 2$, $p < 0.01$). Further analysis was then conducted to see where these differences occurred. Juveniles and sub-adults were found to not be significantly different ($U = 103972$, $n^1 = 308$, $n^2 = 706$, $p > 0.1$). Infants and sub-adults were found to be significantly different ($U = 28432$, $n^1 = 229$, $n^2 = 706$, $P < 0.01$ two-tailed). Infants and juveniles were also found to be significantly different ($U = 12042$, $n^1 = 229$, $n^2 = 308$, $P < 0.01$).

Table 4 shows the percentage of social, play and singing behaviour in different *Hylobatidae spp.* Table 4 highlights the difference between adults and non-adults, especially infants, and displays the low occurrence of social and play behaviours.

Table 4. The percentage of social, play and singing behaviour, during the active period. A comparison between *Hylobatidae spp.*, including the current study. The other studies include some groups that have non-adults, but the data is focused on the adults.

Species	Play	Groom	Sing	Source
<i>Hylobates syndactylus</i>	1	1	1	Gittins and Raemaekers, 1980.
<i>H. lar</i>	0.2	3	3	Gittins and Raemaekers, 1980.
<i>H. agilis</i>	-	-	5	Gittins and Raemaekers, 1980.
<i>H. klossi</i>	-	-	4	Whitten, 1984.
<i>H. pileatus</i>	3	5	4	Srikosamatara, 1984.
<i>H. albibarbis</i>		4	9	Cheyne, in press.
<i>H. albibarbis</i>				Current study
Subadult	5.6		3	
Juvenile	8.7		1	
Infant	41		0.8	

The secondary play behaviours were found to be distributed significantly differently between the three age classes ($H = 16.56$, $df = 2$, $P < 0.01$) (Figure 8.). Sub-adults and juveniles were tested for differences, no significant differences were found ($U = 546$, $n^1 = 29$, $n^2 = 40$, $P > 0.5$). Sub-adults and infants were found to be significantly different ($U = 2150$, $n^1 = 151$, $n^2 = 40$, $P < 0.01$). Juveniles and infants were compared; there was a significant difference between these two age groups secondary behaviour ($U = 1346.5$, $n^1 = 151$, $n^2 = 29$, $P < 0.001$).

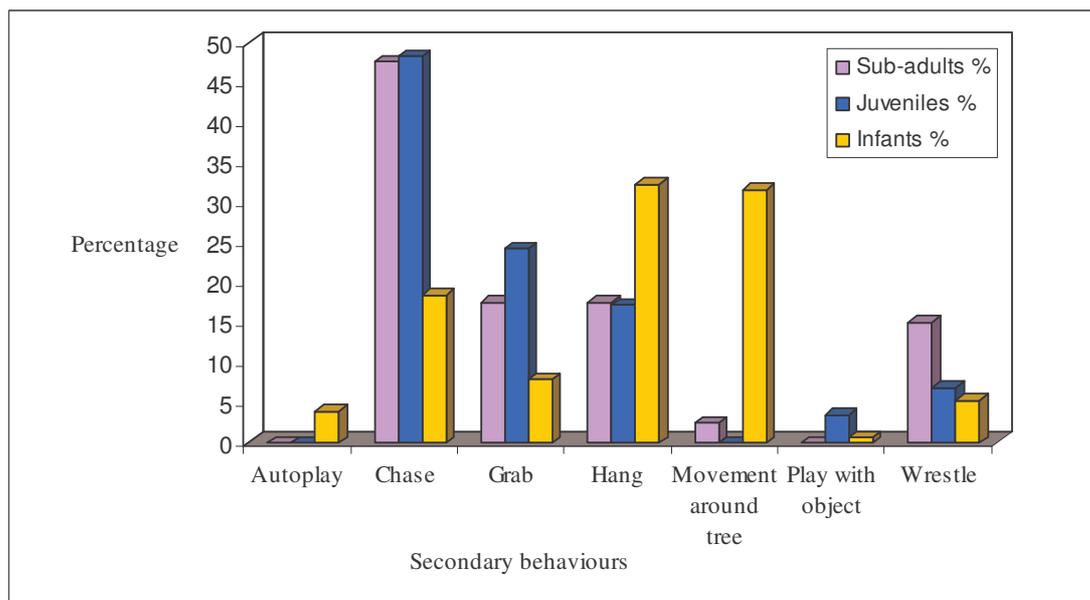


Figure 8. The percentage of secondary play behaviours for sub-adult, juvenile and infant gibbons (*H. albibarbis*), in the LAHG, showing that juveniles and sub-adults show a higher percentage of chase than other play behaviours and infants hang and move around the tree more.

The secondary play behaviours were grouped into two categories: alone or with another gibbon. Sub-adults and juveniles perform a lot more behaviours with a partner than on their own ($\chi^2 = 44.18$, $df = 2$, $P < 0.001$). Infants were found to be statistically different from the sub-adults and juveniles ($\chi^2 = 44.17$, $df = 1$, $P < 0.001$)

The distribution of initiator and focus for play behaviour was not evenly distributed when the three age groups were analysed ($\chi^2 = 5.99$, $df = 2$, $P < 0.05$), showing that the infants initiated play slightly more than the expected count.

Nearest Other Gibbon

The nearest other gibbon, compared by family group, without infants as there were not infants in all three groups, was found to be significantly different in distribution ($\chi^2 = 35.21$, $df = 2$, $P < 0.001$) (Figure 9). Group C individuals were found to spend significantly less time with an adult than expected ($\chi^2 = 30.82$, $df = 1$, $P < 0.001$). Group Karate were found to spend more time with an adult than expected ($\chi^2 = 30.40$, $df = 1$, $P < 0.001$); whilst Group Ninja were not found to have a significantly different distribution ($\chi^2 = 0.22$, $df = 1$, $P > 0.05$).

When the nearest other gibbon was analysed for age, significant differences were found ($\chi^2 = 58.08$, $df = 2$ $P < 0.001$). Infants were then removed as they were highly significant due to higher than expected observations with an adult. Sub-adults and juveniles were compared and no significant difference was found for time spent with an adult or non-adult ($\chi^2 = 1.60$, $df = 1$ $P > 0.05$).

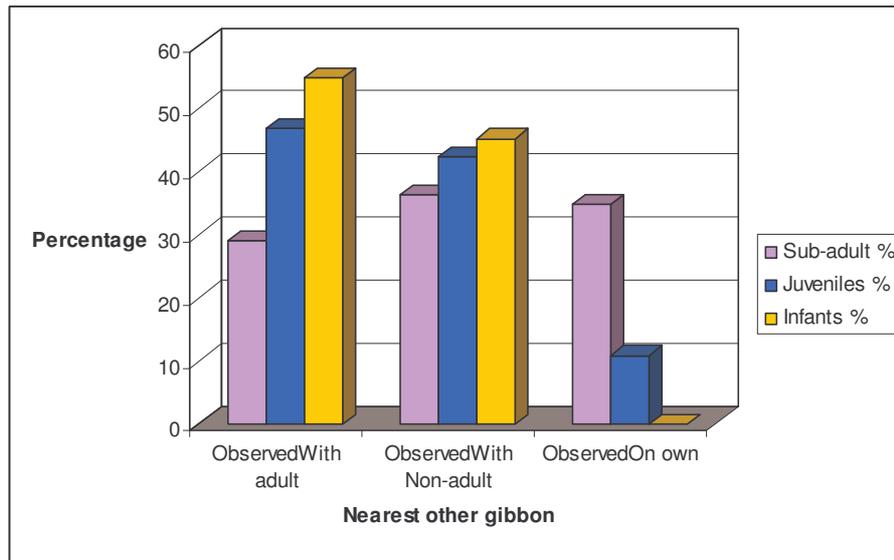


Figure 9. The nearest other gibbon percentage for sub-adult, juvenile and infant gibbons (*H. albibarbis*), in the LAHG; showing that infants were observed with adults for a large percentage of the time, and sub-adults were observed on their own.

Qualitative Findings

During this study qualitative findings were recorded. All play was recorded, even when it occurred outside of the scan samples and unexpected behaviours were also documented. This is a list of some of the findings, a complete set can be found in Appendix 2.

Sub-adult

Play with juvenile or other sub-adult is much more vigorous than when with infant, the higher intensity is reflected in the speed, number of trees used and the strength that is appeared to be used by each individual.

Grooming of the infant by a female sub-adult was witnessed.

Sub-adult male and female brachiated towards a feline animal and followed, chasing it away from the family. This activity happened twice, though the first time it appeared to only be the sub-adult male involved.

Adult female chased female sub-adult away, physical contact seen, grabbing.

Adult male chased female sub-adult away, physical contact, biting on the leg, vocalisation by both.

Juveniles

Chasing of the infant was witnessed, but the infant initiated the play bout.

Juvenile seen squeaking and hanging next to adults while they mate, this is similar in another group but seen in the infant. Juvenile makes squeaking noises and grabs sub-adult, while sub-adult is resting, and pulls.

Infants

Adult female leaves tree, infant squeals, adult female returns and carries to next tree.

Both infants travelled alone for as many as four trees, brachiating and jumping between branches. One infant witnessed crossing trees following the sub-adult male's path.

Both infants try to sing with the group in the morning singing bouts.

One infant seen travelling towards adult female, following adult female's path.

Female infant seen playing on own, swinging towards adult male and grabbing adult male. The adult male reciprocated by grabbing and pulling the infant gently back.

Chapter IV: Discussion

This study was conducted to assess activity budgets in wild non-adult gibbons and to further knowledge about play behaviour in non-adult gibbons. Research into non-adult gibbons is scarce and most of what is known is based on qualitative data observations and data taken from adult studies. The functions of play are subject to debate, but it is generally accepted that play behaviour has an imperative effect on a young animals development. This study found age differences in activity weighting and play behaviour occurrences, with infants appearing to have different behavioural distribution, when compared to sub-adults and juveniles. Some between group differences were found when looking at the nearest other gibbon, and age again appeared to affect the height of the gibbon in the tree and the height of tree used. These will be discussed in more detail and considered with findings from other studies.

Activity Budgets

Knowledge about a species activity budgets can be useful for a variety of reasons and to a variety of people. An animal's general activity budget reflects the importance of activities and how they are weighted when compared to each other. Greater understanding of activity patterns and budgeting will allow for better management for captive animals and allow conservation efforts to be correctly focused for wild animals. Detailed activity budgets allow changes in the activity distribution to be noted and possible ecological or man-made reasons for these changes to be assessed (Stockwell *et al.*, 1991; Orams, 2002). As little is known about non-adult gibbons it is imperative that research is done so that these understudied animals can be understood and their habitats protected effectively.

Activity budgets differed significantly between sub-adults, juveniles, and infants. This is not surprising as infants were still being carried ventrally by their mothers and therefore their travel and rest was dependant on the mothers' activity patterns. Due to their young age, infants may not be observed feeding as much as they were not weaned so would still have been nursing, which is harder for an observer to see and is likely to occur when the adult female is resting. Between group findings suggest that

there is low group variation for non-adults. This is different to findings from studies concerned with adult activity budgets. Cheyne (in press) found that “groups without ventral infants fed more and groups with ventral infants rested more”. Similar between group differences were also noted by Bicca-Marques and Calegario-Marques (1994) in *Aloutta caraya*. The arguments for such differences between groups seem to focus on group composition. The presence of infants appears to have a large effect on activity budgets, it could be that the distance travelled is less but that the time travelling is more, as infants will slow down travelling whether they are being carried or travelling alone. Carrying infants is thought to be energetically costly, second only to nursing (Altman and Samuels, 1992), it is also true that when the infants begin to travel by themselves they will still move slower and will not be able to choose routes as well or as quickly as their older counterparts. For this study each group had a different composition, so it could be assumed that between group differences would be found, but the similarities between groups may be more representative of the importance of the activities and the lack of control that non-adults have on the groups activities. Group C did not have an infant, but the juvenile and sub-adult are thought to be younger than their counterparts in the other groups. This may mean that the adults’ activity is still affected by their presence. Amounts of play were found to not differ between groups; it is possible that this is because of when play occurred. Play behaviour may be opportunistic in gibbons as they are arboreal and often move quickly from feeding tree to feeding tree, meaning the infant must sometimes stay close to the mother; so play may occur more during rest periods or extended feeding times, which could counteract the between group differences found in adults. Adult activity budgets have been extensively studied in a diverse range of animals (Bernstein and Schusterman, 1964; Marsh, 1981; Prince and Francis, 1984; Bicca-Marques and Calegario-Marques, 1994; Chiarello, 1998), but non-adult budgets are still understudied.

One of the main findings that the activity analysis revealed was the decrease in play behaviour with the age of gibbon. This will be discussed further in the next section, the only activity infants undertook more than play was clinging to the mother, it must be remembered that this would include most of their travel time. However, play was still remarkably high even when this is considered.

When the non-adult behaviour was compared with adult behaviour it was found that sub-adults were most similar to adults in the distribution of their behaviour. This is not surprising as they are reaching sexual maturity, will be encouraged to be more independent and will need to start taking an active role in route planning and finding feeding trees. Qualitative findings showed sub-adults often took very different routes to the adults and fed, sometimes for sustained periods, from trees that were more than twenty metres away from the adults. Juvenile behaviour is more similar to sub-adult behaviour, than infants, in distribution. Again this is unsurprising as they are travelling alone and will begin to make decisions for themselves, though qualitative findings suggest that they still follow the adult female closely and will generally feed in the same or a very close tree.

The differences between non-adults and adults activity budgets are important as they highlight the different needs and developmental stages of young gibbons. Knowledge of this kind can help highlight the plight of gibbons with regards to the pet trade; and provide more information for rescue and rehabilitation centres and zoos about the activity budgets of gibbons. Showing the amount of time spent feeding and travelling helps to show how much of their day is taken up with these activities. Previous research, on various animals, suggests that inappropriate husbandry, barren rearing environments and insufficient foraging opportunities can have an effect on abnormal behaviours (Erwin and Deni, 1979; Anderson and Chamove, 1985; Flurer and Zucker, 1988; Nash *et al.*, 1999; Cheyne, 2004, 2007d). Abnormal and stereotypic behaviours are often displayed by animals in captivity and are thought to be reflective of inadequate welfare. Abnormal behaviours in gibbons have been recorded to include coprophagy, masturbation, self injurious behaviour and abnormal or underdeveloped calling or singing (Mootnick and Baker, 1994; Cheyne, 2004, 2007d; Hosey and Skyner, 2007; Shepherdson *et al.*, 2007; Cheyne *et al.*, 2007a). From the results of this study it can be seen that non-adult gibbons only spend, at most, 29% of their time resting. This demonstrates the need for other activities to take up the majority of their time during the day, meaning that these needs must be provisioned for. As gibbons are predominantly arboreal housing for captive gibbons must reflect this need. Gibbons territories in the LAHG average forty-seven hectares and the groups are thought to range on average 2433m a day (Cheyne, in press). This space cannot be adequately provisioned for in captivity, but the time spent travelling must be taken

into consideration and appropriate measures taken to provide opportunities for arboreal movement and foraging. Knowledge about activity budgets and gibbons daily activities will allow for better and more appropriate provision for captive gibbons.

The infants' activity budgets show they spend most of their time clinging to the mother, followed closely by playing. Though information on the mothers' activity while this happened was collected it was not analysed as it would not further the findings of this project. The high percentage of play behaviour witnessed is interesting because social behaviour was thought to be low in gibbons (Ellefson, 1974). It is possible that the small sample size is responsible for the high levels of play shown; but it is more likely that gibbons do participate in play frequently, like other mammals. A more detailed and longitudinal study would be needed to fully understand the play behaviour of gibbons, the focus of such studies will be discussed later.

The analysis of secondary play behaviour showed some valuable findings. Juveniles and sub-adults were found to play significantly more with a partner than without. This finding supports previous findings into play behaviour and highlights the likelihood that self-handicapping was being implemented (Spinka et al., 2001).

Play Behaviour

Play behaviour has always been a contentious subject; whether it exists, how to define it and what the costs and benefits are. The costs and benefits range from immediate and delayed; with most accepting that the noticeable lack of immediate benefit is a defining characteristic of play (Bekoff and Byers, 1981). Play is variable between and within species (Poirier and Smith, 1974), with the focus of play and amount of time spent on the activity differing. Poirier (1969a, 1970) found differences between north and south Indian langurs (*Semnopithecus spp.*), though these are now considered two separate species which could account for some of the difference; and Bekoff (1972) discusses the different functional roles of play for a variety of mammals. The reasons for play appear to be varied, ranging from motor and cognitive development, bonding, practice for coping with unexpected events and

positive feelings elicited by the behaviour (Darwin, 1874; Harlow, 1965; Bekoff, 1972, 2001). The importance of play cannot be ignored, if play is absent from an animals repertoire it can reflect external pressures. Knowledge about play in the wild could help to assess the welfare standards of animals in captivity. By using amount of play, types of play observed and the partners involved it can be possible to determine normal amounts of activity in captive animals, and also to help to house animals with appropriate conspecifics.

Costs and benefits of play behaviour could be the centre-point of the play argument, as they are central to the function of play. The costs of play include energy use, predation risk, self-handicapping and less time to perform other activities (Caro, 1995). The benefits of play include social bonding, motor and cognitive development, increased knowledge of social boundaries, preparing for the unexpected and knowledge that will aid the young animal later (De Oliviera et al., 2003). Usually it is thought that the benefits must outweigh the costs for an action to be ecologically viable; however, with play the costs and benefits may not be directly comparable as some will be immediate and others delayed; herein lies the problem when considering play behaviour. Though there is undoubtedly a cost to play behaviour, it may not be large. Young animals' time constraints are not the same as adults, this is especially true of infants, and they may not require the same amount of food to fuel them as adults. If this is the case an infant, who for the majority of travelling is clinging to the mother, may have more energy and time to use than an adult, sub-adult or juvenile.

The analysis of the gibbons play behaviour showed numerous differences between infants and the two older age groups of gibbon. The infants conducted significantly more play, in comparison to other activities, than either the juveniles or sub-adults. The non-adults all showed higher rates of play behaviour than adults when compared to other *Hylobatidae* species. However, these comparisons must be drawn tentatively, as play often has different definitions and different data collection techniques. Despite this the findings are not surprising, as young animals are thought to “spend little or no time engaging in adult activities such as mating, hunting, or defending territory and are probably less constrained by time and energy considerations than adults of the same species” (Martin and Caro, 1985, p. 81). The play decreased with age, with sub-adults approaching adult proportions of play, this could be due to sub-

adults beginning to include more adult behaviours in their repertoire; for example, territory defence and finding food. This study compounds findings in numerous other species; for example, Poirier and Smith (1974) state that play decreases with age and Frisch (1968) discusses how young Japanese macaques (*Macaca fuscata*) are more explorative than their older counterparts. It is also thought that young animals are more elastic in their behaviour and this flexibility encourages explorative behaviours, like play (Tsumori, 1967; Frisch, 1968; Poirier and Smith, 1974). Play is considered explorative as it allows an animal to practice and investigate behaviours and substrates before needing to use them in a real situation. The juvenile period in primates is longer than most mammals (Joffe, 1997) and it has been shown that the further up the phylogenetic tree the longer the adolescence in primates is (Schultz, 1956, 1969). Poirier and Smith (1974, p.276) found that “the juvenile period in lemurs is approximately two years, in macaques it is four years, in chimpanzees eight years, and among *Homo sapiens* the juvenile period is extended to sixteen years.” This extended time suggests that it is an important period and will probably have a great effect on future behaviours. Cheyne (2009c) suggests that it is likely that there is a sensitive period in young gibbons, and that within this time they are highly motivated to attempt novel tasks. The decrease in play with age could be affected by the energy and time expenditure used to travel and feed more. When the infant matures enough to stop being carried by the mother and to stop nursing, more food will be needed to gain enough energy to compensate these changes. Another possible reason could be the increasing reliance of the adults on the older offspring to defend the territory; this type of territory defence was recorded in the qualitative findings and is documented in other studies (Reichard and Sommer, 1997). Sub-adults are thought to be tolerated in groups, sometimes after reaching sexual maturity, because they can aid the adults in group and territory defence, meaning a group may be able to expand their existing territory or prevent another group from encroaching on their territory more successfully (Reichard and Sommer, 1997). Play will have an energetic cost, as do all behaviours; but the extent of this cost is debated (Martin and Caro, 1985). It is often documented that when an animal is placed under environmental pressures, for example a lack of food, play is one of the first behaviours to be dropped from a repertoire, possibly due to cost/benefit ratio (Muller-Schwarze et al., 1982; Panksepp et al., 1984). However, it is also recorded that young animals spend a lot of time and

energy playing (Bekoff, 1972; Fagen and George, 1977); the findings of the current study are in line with these ideas.

Juveniles and sub-adults were found to not have a statistical difference in their activity distribution, within or between age groups. It appears that the infants have the most varied behaviour. It is not surprising that infants differed from sub-adults and juveniles, play and clinging to mother took up the largest percentage of their activity. Obviously travelling will be lower in infants because they travel with the mother. The secondary behaviour when the infants were clinging to the mother were recorded, but were not used for the analysis, as this behaviour was the mothers choice not the infants. However, even when clinging to mother was included the percentage of play was still large (Table 4) in comparison to the other non-adults and adults from other species.

Infants are likely to play more for a variety of reasons. Less energy being used for travelling and feeding has already been mentioned, motor and cognitive development must be considered. If it is true that there is a sensitive period of development that play needs to occur within, then it would appear logical that infants will play more than other age groups (Byers and Walker; 1995; Hol *et al.*, 1999). When an animal is young their brain pathways are elastic and will become stronger and the neurons will travel quicker if they are used more frequently (Panksepp, 1981; Byers and Walker, 1995). This is another valid reason for play occurring more in infants, as in juveniles and sub-adults the motor-neuron pathways are likely to be more fixed. The concept of play preparing an animal for later in life would also explain the decrease in solo-play and the focus shifting to partner orientated play. Partner orientated play will put the player under pressure whilst putting the player in a variety of positions and situations. This will be more useful to a fast moving gibbon than just moving around the tree by themselves. Moving around a tree alone will be useful for infants as it will develop their ability to travel alone, but once they are travelling alone they will need something more challenging. Playing alone for an infant will be part of the exploration of their surroundings and their abilities. Not only does play help to develop brain pathways it helps develop muscle as well. Byers and Walker (1995) suggest that there is a sensitive period for muscle fibre development, and that play can help develop these muscle fibres. Play uses motor-patterns and muscles that will be needed in everyday life; for gibbons play, including chasing and moving around the

tree, allows the infant to practice behaviours that will soon be imperative to their survival.

The secondary characteristics of play behaviour were found to be distributed significantly differently between age groups. Juveniles and sub-adults played significantly more with a partner than on their own, suggesting a shift in play dynamics and focus for non-adult gibbons, as with the infants it was a more even split. It could be that the older gibbons play becomes more focused on emulating behaviours that they need, though this is unlikely as most play behaviours reflect 'real' behaviours to some extent, or that they have less time to play as more is taken up with feeding and travelling, so possibly play becomes something they are drawn into by another. It is also likely that, as Boulton and Smith's theory (1992) states, each animal must make a sacrifice to play. It is possible sub-adults and juveniles will be inhibiting their strength, self-handicapping, in order to play with the infants. Playing with infants may not be as rewarding for the older gibbons physical development, but they could be facilitating play to benefit the infant. They will also receive some benefits, even if it is just a positive feeling from an internal feedback system. It is also thought play promotes bonding between the players (Bekoff, 2001); this would be especially important for sub-adults as they are moving towards adulthood and will either soon or already start to be forced from the group. Bonding with an infant may make the adults more tolerant of their presence in the group.

Overall play was found to be prevalent in all age groups, though infants were shown to play more frequently than the other two age groups. This study is limited as it has a small sample size and was conducted over a short time period. However, it has shown that non-adult gibbons do play and that they therefore have social behaviour, possibly to higher percentages of their overall activity budget than expected.

Tree Heights and Gibbon Height in the Tree

Sub-adults used a higher proportion of high canopy trees than juveniles and infants. Infants appear to use middle sized trees a disproportionate amount of the time and spend little time in very low or very tall trees. The tree heights used for play behaviour did not show a statistically significant difference. Tentative ideas can be

formed from these findings; for example, infants may be safer in the middle height trees as they will not have as far to fall, if they did fall; the mothers do not have to climb as high while carrying an infant, but will be safer from some predators than if they were in the very low trees. However, more information can be gained from the analysis of the height of the gibbons in the trees, as this shows how high gibbons were when observed. The analysis showed that juveniles again used the trees as expected, but sub-adults and infants did not. Sub-adults used the upper canopy levels (>20m) more than expected and infants used them less. Infants also used the lower canopy levels of trees less (<10m), but again used the middle heights (16-20m) significantly more than would be expected by chance.

Between group differences were also found, showing that Group Ninja used the top canopy less than would be expected, while Group C used the lower level less than expected. The difference between Group Ninja and the other two groups is surprising as there are two sub-adults in the group, and it was shown that sub-adults seem to spend more time in the higher canopy than the other two age groups; but Group Ninja had an infant present, so this may account for the difference, as infants were not found to use the lower heights if the trees.

There are problems with these findings, however; as with the other findings of this study the sample size and duration of the study is small. The other problem for the tree height and height of gibbon in the tree is the forest. The LAHG was commercially logged for thirty years and then illegally for about ten years, meaning that the area this study was conducted in is secondary, mixed-swamp forest (Cheyne, 2009b). This will affect the results as the distribution of the tree heights may not be as would be expected in a pristine forest. It is difficult to make inferences from the data as habitat and forest assessments were not carried out for this study, if the tree heights were assessed for the gibbon territories the data would be more meaningful, as this could be adjusted for and taken into consideration in the overall findings. However, the findings for the height of the gibbons in the tree are valid even without overall habitat analysis as it is concerned with the placing of gibbons rather than heights of the trees. When interpreting the data it must also be remembered that infants do not select a large majority of the trees or height where they spend their time, as they were both still travelling with the mother and sometimes rested with her as well.

Nearest Other Gibbon

The nearest other gibbon is of interest as it will show if a shift occurs in the closest other gibbon with age. The observations were separated into: with an adult, with a non-adult or alone, as the data set was relatively small and this was deemed to be more valid. When family groups were analysed, without the infants as there were not infants in each group, a significant difference was found. Group C juveniles and sub-adults were found to spend significantly less time with an adult, Group Karate were found to spend more time with an adult than expected, while Group Ninja's juveniles and sub-adults did not have a significantly different distribution. When age differences were analysed a significant result was found, the infants were found to have higher than expected observations with adults, this was when observations of them clinging to mother had been removed. The infants were then removed from the analysis and sub-adults and juveniles were compared. No significant difference was found between the older two age groups, showing that it is the infants that have a disproportionate observation count. This is as would be expected for although the infants played with the juveniles and sub-adults, they are still dependant on the mothers and would not spend extended periods of time away from the mothers.

Qualitative Findings

Though the qualitative data are not quantifiable the observations could help to focus future research and highlight areas of interest. Over the course of the study play behaviour, involving chasing and wrestling, between sub-adults and juveniles appeared to be more physical, faster paced and of higher intensity than when older non-adults engaged in play with an infant. These findings could be linked to the theory of self handicapping. Spinka *et al.* (2001) discuss how self-handicapping can be used by an older, bigger or stronger animal to allow them to play safely with a smaller conspecific. This idea could be imperative for gibbon play as there are large inter-birth intervals (Mitani, 1990; Geissmann and Thanh, 2001). If an older gibbon does not implement self-handicapping the result could mean injury for the younger primate, or the cessation of play and possible lack of restarting. For if play causes injury or does not allow a player to participate fully they are unlikely to play with that partner again. This idea links to Boulton and Smith's (1992) discussion on the costs involved in playing with another animal; for example, when wrestling one animal

compromises and will be the partner that is “pinned”, this player may not get as much benefit from this as the other player, because they are not getting to practice the dominant behaviour, but they will get to play again; reciprocal altruism is being instigated (Trivers, 1971). If an animal was consistently preventing the other from being the “chaser” or the dominant one in wrestling it is likely they would not play very often and both players would miss out on playing (Boulton and Smith, 1992). This is likely to be particularly true of gibbons as they have limited partner access, due to their small group size (Tenaza, 1975; Cheyne, in press). It would appear imperative for the infant gibbons that the sub-adults and juveniles implement self-handicapping so that they can play safely and frequently. As play also promotes social bonds it is likely that this will happen.

The investigation and ultimate chase of a feline animal by two sub-adult gibbons in a group was witnessed during the study. This occurred twice in one day, with both sub-adults coming low in the trees and following the animal out of sight. This sighting could be evidence for the benefits of having sub-adults in a group and could highlight possible reasons that extra-adult families exist (Brockelman *et al.*, 1998). It is possible the added defence benefits to a group of a sub-adult, and sometimes adult, offspring remaining with the family group outweigh the costs of finding enough food for a larger group. Care giving and defence by siblings have been documented in a variety of species; including birds and primates (Chapais *et al.*, 2001; Griffin and West, 2003). This idea was first introduced by Axelrod and Hamilton (1981), when they discussed kin altruism. The theory behind kin altruism is that the “helper” will gain an indirect fitness benefit by aiding in the rearing and ultimate survival of their relatives (Chapais and Bélisle, 2004). Kin selection suggests costs to the helper; for example, not breeding, are outweighed by group living benefits and the shared genetics of the offspring they are helping care for (Cheverud, 1984; Clutton-Brock, 2002). Sub-adults helping in territory and group defence will be especially useful for gibbon groups when infants are present. As the mother spends a high proportion of time carrying the infant, she may be less able or likely to actively participate in aggressive encounters.

The qualitative findings appear to suggest that play behaviour, especially for infants, is opportunistic. Whilst the mother feeds, infants would play on their own around the

tree, maybe with an older sibling if they were near. During rest periods it was often seen that an infant and a conspecific would play together. The infant appeared to play with another partner when the mother was resting or feeding for extended periods of time. These observations are not quantifiable from the study conducted; but could be analysed if observations of adults and young were taken simultaneously. Although this did happen for some of this study, the data set is not large enough to carry out statistical tests on. This idea seems viable as, because the infant travels with the mother, the infant cannot move too far away from the mother when she is not feeding or resting for a sustained period of time. This also highlights the meta-communication between gibbons, vocalisation does occur but it is not frequent, meaning that other forms of communication and understanding are occurring (Gittins and Raemaekers, 1980).

One qualitative finding that does not seem to fit with the statistical findings is that sub-adults were found in the lower canopy (<10m) often. However, one reason for the lack of statistical data may be due to the short periods of time spent at this level, it appeared they were either opportunistically feeding or being vigilant. As the data was collected using five minute scan samples these bouts in the low levels of the tree could have been missed. It is thought that sub-adults help with territory and group defence, they also feed in different trees and make route decisions more independently than the younger gibbons. Further study would be needed to see if they were found in the lower parts of the tree more often than the other parts of the trees or than other age groups of gibbons.

Over the course of this study attempts appeared to be made to force the female sub-adult in Group Karate to disperse. Various aggressive encounters from the adult female were encountered and one from the adult male resulting in physical aggression. This last observation is unusual as it is generally thought that the same-sex parent will force the sub-adult out (Brockelman *et al.*, 1998). The process by which sub-adults leave a group is understudied as they are very difficult to follow and require long-term studies; this is true of most mammals (Pusey and Packer 1987; Brockelman *et al.*, 1998). However, as the sub-adult in question is habituated it is hopeful that if a new group is formed some following may be able to happen if they find territory in the existing research grid within the LAHG.

Chapter V: Conclusion

Future Research

Activity Budgets

Gathering more detailed activity budgets would be useful; with a larger sample size the age differences may be even more pronounced. Sex differences may also be identified with a larger sample size. Another factor that would be interesting to consider is seasonal variation. The LAHG floods annually (Page *et al.*, 1999b) this and fruiting patterns may affect the young gibbons behaviour, as the foods in adult diets have been found to be highly variable depending on the season (Cheyne, in press). Further research would also be needed into the habitat, as habitat analysis and average tree height densities for the gibbon territories would allow more accurate conclusions to be drawn from the height of the gibbon in the tree data.

Play Behaviour

The play behaviour analysis was an important part of this study; it could be looked at in even more detail, with duration of play bouts, time of day and a comparison with what the rest of the family are doing when play occurs being analysed. The initiator and focus part of the play behaviour analysis would be able to be analysed more comprehensively with a larger sample size and more data points. This is an interesting area of research as who initiates the behaviour could determine social boundaries and hierarchies. Though hierarchies are not relevant for gibbon behaviour, it is interesting to look at the age effects on the initiator and focus aspect of play. It again would be interesting to do a longitudinal study and correlate seasonal fruiting patterns with play behaviour and see if there is any effect.

Sub-adults

The sub-adults in each of the group were an interesting and more difficult age group to study. More in depth research with a larger sample size could investigate the dispersal patterns of the sub-adults, their height in the tree as they travel and feed and their involvement in territory and group protection.

Conservation Implications

Though behavioural studies are often thought to be separate from conservation studies, this does not have to be the case (Sutherland, 1998). Research focusing on activity budgets is of the utmost importance as it allows a detailed picture of the animals' needs and habitat use to be constructed; enabling more accurate and focused protection. It also allows for easier identification of possible threats to the animal and the ability to monitor changes in the habitat and the effects these are having on the animals. Research detailing non-adult primates' activity and behaviour highlights their importance for the group survival and dynamics. The importance of play and the opportunity for social behaviours on young primates' development have been shown to be large (Poirier and Smith, 1974; Palagi *et al.*, 2004; Cheyne, 2006), showing that groups must be protected so that the young can develop into fully-functioning adults.

Captive Management

The aims of this study were to help further knowledge about an understudied age group. Non-adults are often found in captivity, in Indonesia they often end up in rescue centres when they have been confiscated from the illegal pet trade (Nijman, 2005). As the mother is usually killed, when an infant is taken from the wild, most grow up in captivity without contact with an adult gibbon. This study helps to highlight the importance of familial interactions for young gibbons, and demonstrates that even when they are nearly fully mature they still have an integral role in the family. Housing gibbons correctly and providing adequate resources and social contact is imperative to young, and adult, gibbons' development and well-being.

The aims of this research were to further knowledge about an understudied species and age group, non-adult *Hylobates albibarbis*; focusing on their behaviour, which, until now, has been severely understudied. The study sample is obviously small and the period of research short; but even in this short time interesting findings regarding age differences were found. The study also showed that it is possible to conduct detailed behavioural research on non-adult gibbons. This study is, as mentioned, just an exploratory look into the complicated behavioural intricacies of non-adult gibbons, there is still huge scope for future research. The fact that play behaviour occurs at high levels in gibbons is a huge step forward in understanding these small apes, it is also important that their cognitive abilities are acknowledged. Though in the past

they have been thought to demonstrate low amounts of social and play behaviour compared to other apes, this is possibly not true if the non-adults are focused on. Play and exploration is often used as a research tool indicative of cognitive ability (Cheyne, 2009c). This area of study would benefit from further research, as it seems likely that if lower amounts of play are witnessed in gibbons when compared to other primates, it could be due to their arboreal nature and family dynamics, rather than lower cognitive ability. This study highlights the importance of more research into these understudied apes and takes a small step towards the recognition these small apes deserve.

References

- Aldis, O., 1975. *Play fighting*. Academic Press, New York.
- Altman, J., 1974. Observational study of behaviour: sampling methods. *Behaviour*, 49(3/4), 227-267.
- Altmann, J. and Samuels, A., 1992. Costs of maternal care: Infant-carrying in baboons. *Behavioural Ecology and Sociobiology*, 29(6), 391-398.
- Anderson, J.R. and Chamove, A.S. 1985. Early social experience and the development of self-aggression in monkeys. *Biological Behaviour*, 10, 147-157.
- Appleby, D.L., Bradshaw, J.W.S. and Casey, R.A., 2002. Relationship between aggressive and avoidance behaviour by dogs and their first six months of life. *The Veterinary Record*, 150(14), 434-438.
- Axelrod, R. and Hamilton, W.D., 1981. The evolution of cooperation. *Science*, 211, 1390-1396.
- Baldwin, J.D and Baldwin, J.I., 1974. Exploration and social play in squirrel monkeys (*Saimiri*). *American Zoologist*, 14, 303-315.
- Bartlett, T. Q., 2001. Extra-group copulations by sub-adult gibbons: implications for understanding gibbon social organisation. *American Journal of Physical Anthropology*, 32 (supplement), 36.
- Bartlett, T.Q., 2003. Intragroup and Intergroup Social Interactions in White-Handed Gibbons. *International Journal of Primatology*, 24(2), 239-259.
- Bekoff, M., 1972. The Development of social interaction, play, and metacommunication in mammals: An ethological perspective. *The Quarterly Review of Biology*, 47(4), 412-434
- Bekoff, M., 1984. Social play behaviour. *Bioscience*, 34(4), 228-233.
- Bekoff, M., 2001. Social play behaviour. Cooperation, fairness, trust, and the evolution of morality. *Journal of consciousness studies*, 8(2), 81-90.
- Bekoff, M. and Byers, J.A., 1981. A critical reanalysis of the ontogeny of mammalian social and locomotor play: An ethological hornet's nest. In: Immelmann, K., Barlow, G.W., Petrinovich, L. and Main, M., eds. *Behavioural development: The Bielefeld interdisciplinary project*. Cambridge University Press, New York, 296-337.
- Bernstein, I.S. and Schusterman, R.J., 1964. The activity of gibbons in a social group. *Folia Primatologica*, 2, 161-170.
- Biben, M., 1998. Squirrel monkey play fighting: making the case for a cognitive training function of play. In: Bekoff, M. and Byers, J.A., eds. *Animal play*:

evolutionary, comparative and ecological perspectives. Cambridge Press, England, 161-182.

Bicca-Marques, J.C. and Calegario-Marques, C., 1994. Activity Budget and Diet of *Alouatta caraya*: An Age-Sex Analysis. *Folia Primatologica*, 63(4), 216-220.

Birkhead, T. R. and Møller, A. P., 1995. Extra-pair copulation and extra-pair paternity in birds. *Animal Behaviour*, 49(3), 843-848

Boulton, M.J. and Smith, P.K., 1992. The social nature of play fighting and play chasing: mechanisms and mechanisms and strategies underlying cooperation and compromise. In: Barkow, J.H., Cosmides, L. and Tooby, J., eds. *The adapted mind, evolutionary psychology and the generation of culture*. Oxford University Press, England, 429-451.

Brandon-Jones, D., Eudey, A.A., Geissmann, T., Groves, C.P., Melnick, D.J., Morales, J.C., Shekelle, M. and Stewart, C.B., 2004. Asian Primate Classification. *International Journal of Primatology*, 25(1), 97-164.

Brockelman, W. Y. and Ali, R., 1987. Methods of surveying and sampling forest primate populations. In: Marsh, C.W. and Mittermeier, R.A. eds. *Primate Conservation in the Tropical Rain Forest*. Alan R. Liss, New York, 23-62.

Brockelman, W.Y., Reichard, U., Treesucon, U. and Raemaekers, J. J., 1998. Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behavioural Ecology and Sociobiology*, 42(5), 329-339.

Buckley, C., Nekaris, K.A.I. and Husson, S.J., 2006. Survey of *Hylobates agilis albibarbis* in a logged peat-swamp forest: Sabangau catchment, Central Kalimantan. *Primates*, 47, 327-335.

Byers, J.A. and Walker, C., 1995. Refining the motor training hypothesis for the evolution of play. *The American naturalist*, 146(1), 25-40.

Caro, T.M., 1995. Short-term costs and correlates of play in cheetahs. *Animal Behaviour*, 49, 333-345.

Chapais, B. and Bélisle, P., 2004. Constraints on kin selection in primate groups. In Chapais, B. and Berman, C.M., eds. *Kinship and behaviour in primates*. Oxford University Press, Oxford, Part iv, ch. 13, 365-386.

Chapais, B., Savard, L. and Gauthier, C., 2001. Kin selection and the distribution of altruism in relation to degree of kinship in Japanese macaques (*Macaca fuscata*). *Behavioural Ecology and Sociobiology*, 49(6), 493-502.

Cheverud, J.M., 1984. Evolution by kin selection: a quantitative genetic model illustrated by maternal performance in mice. *Evolution*, 38(4), 766-777.

Cheyne, S.M., 2004. Assessing rehabilitation and reintroduction of captive-raised gibbons in Indonesia. (PhD). University of Cambridge, Cambridge.

Cheyne SM, 2006. Gibbons: conservation and the future for the world's smallest ape. *Edinburgh University Graduate Association Journal*, 159-162.

Cheyne, S.M., 2007d. Unusual behaviour of captive-raised gibbons: implications for welfare. *Primates*, 47, 322-326.

Cheyne, S.M., 2008b. Feeding ecology, food choice and diet characteristics of gibbons in a disturbed peat-swamp forest, Indonesia. In: Lee, P.C, Honess, P., Buchanan-Smith, H., MacLarnon, A. and Sellers, W.I., eds. *22nd Congress of the International Primatological Society (IPS) Edinburgh, UK: Top Copy, Bristol*; 342.

Cheyne, S.M., 2009b. Forest Fires in Indonesia. In: *The Wanderer*. Oxford.

Cheyne, S.M., 2009c. Studying Social Development and Cognitive Abilities in Gibbons (*Hylobates spp*): methods and applications. In: Potocki, E. and Krasiński, J. eds. *Primateology: Theories, Methods and Research*. Nova Science Publishers, New York.

Cheyne, S.M., in press. Behavioural ecology and socio-biology of gibbons (*Hylobates albibarbis*) in a degraded peat-swamp forest. In: Supriatna, J. and Gursky, S.L., eds. *Indonesian Primates*.

Cheyne, S.M. and Brulé, A., 2004. Adaptation of a captive-raised gibbon to the wild. *Folia Primatologica*, 75, 37-39.

Cheyne, S.M., Chivers, D.J. and Sugardjito, J., 2007a. Covariation in the great calls of rehabilitant and wild gibbons *Hylobates agilis albibarbis*. *Raffles Bulletin of Zoology*, 55, 201-207.

Cheyne, S.M., Thompson, C.J.H., Phillips, A.C., Hill, R.M.C. and Limin, S.H., 2007b. Density and population estimate of gibbons (*Hylobates albibarbis*) in the Sabangau catchment, Central Kalimantan, Indonesia. *Primates*, 49, 50-56.

Cheyne, S.M., Chivers, D.J. and Sugardjito, J., 2008. Biology and Behaviour of Released Gibbons. *Biodiversity and Conservation*, 17, 1741-1751.

Chiarello, A.G., 1998. Activity budgets and ranging patterns of the Atlantic forest maned sloth *Bradypus torquatus* (Xenarthra: Bradypodidae). *Journal of Zoology*, 246, 1-10.

Chivers, D. J. 1977. The ecology of gibbons: some preliminary considerations based on observations in the Malay Peninsula. In: *The use of non-human primates in biomedical research*. eds. M. R. N. Prasad and T.C. Anand Kumar. Indian Science Research Academy, New Delhi, 85-105.

Chivers, D.J. and Raemaekers, J.J., 1980. Long term changes in behaviour. In: Chivers, D.J., ed. *Malayan Forest Primates: Ten years study in tropical forest*. Plenum Press, New York, 109-160.

Clutton-Brock, T., 2002. Breeding Together: Kin Selection and Mutualism in Cooperative Vertebrates. *Science*, 296(5565), 69-72.

Cowlshaw, G. 1992. Song function in gibbons. *Behaviour*, 121(1-2), 131-153.

Curran, L. M., Trigg, S. N., McDonald, A. K., Astiani, D., Hardiono, Y. M., Siregar, P., Caniago, I. and Kasischke, E., 2004. Lowland forest loss in protected areas of Indonesian Borneo. *Science*, 303, 1000-1003.

Darwin, C., 1874/1998. *The descent of man; and selection in relation to sex*. Prometheus books, New York.

De Oliveira, C.R., Ruiz-Miranda, C.R., Kleiman, D.G. and Beck, B.B., 2003. Play Behavior in Juvenile Golden Lion Tamarins (*Callitrichidae: Primates*) [*Leontopithecus rosalia*]: Organization in Relation to Costs. *Ethology*, 109, 593-612.

DiPietro, J.A., 1981. Rough and Tumble Play: A Function of Gender. *Developmental Psychology*, 17(1), 50-58.

Ellefson, J. O., 1974. A natural history of white handed gibbons in the Malayan peninsula. *Gibbon and Siamang*, 3, 1-136.

Erwin, J. and Deni, R., 1979. Strangers in a strange land: abnormal behaviours or abnormal environments? In: Erwin, J., Maple, T.L. and Mitchell, G. eds. *Captivity and behaviour*. Van Nostrand Reinhold Co., New York, 1-28.

Fagen, R., 1974. Selective and evolutionary aspects of animal play. *The American Naturalist*, 108(964), 850-858

Fagen, R.M., 1981. *Animal play behaviour*. Oxford University Press, New York.

Fagen, R.M. and George, T.K., 1977. Play behaviour and exercise in young ponies (*Equus caballus L.*). *Behavioural Ecology and Sociobiology*, 2, 267-269.

Felton, A.M., Engstrom, L.M., Felton, A. and Knott, C.D., 2003. Orang-utan population density, forest structure and fruit availability in hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia. *Biological Conservation*, 114, 91-101.

Flurer, C.I. and Zucker, H., 1988. Coprophagy in marmosets due to insufficient protein (amino acid) intake. *Laboratory Animals*, 22, 330-331.

Fry, D.P., 1987. Differences between play-fighting and serious fights among Zapotec children. *Ethology and Sociobiology*, 8, 285-306.

Freedman, D.G., King, J.A. and Elliot, O., 1961. Critical period in the social development of dogs. *Science*, 133 (3457), 1016-1017.

Frisch, J., 1968. Individual behaviour and intertroop variability in Japanese macaques. In: Jay, P., ed. *Primates: studies in adaptation and variability*. Holt, Rinehart & Winston, New York, 243-253.

Geissmann, T., 2007. Status reassessment of the gibbons: Results of the Asian Primate Red List Workshop. *Gibbon Journal*, 3, 5-15.

Geissmann, T. and Orgeldinger, M., 2000. The relationship between duet songs and pair bonds in siamangs, *Hylobates syndactylus*. *Animal Behaviour* 60, 805-809.

Geissmann, T. and Thanh V. N., 2001. Preliminary results of a primate survey in northeastern Vietnam, with special reference to gibbons. *Asian Primates*, 7(3-4), 0-4.

Gittins, S.P., 1982. Feeding and Ranging in the Agile Gibbon. *Folia Primatologica*, 38, 39-71

Gittins, S.P. and Raemaekers, J.J., 1980. Siamang, Lar and agile gibbons. In: Chivers, D., ed. *Malayan forest primates*. Plenum Press, New York. Ch. 3, 63-105.

Griffin, A. S. and West, S.A., 2003. Kin Discrimination and the Benefit of Helping in Cooperatively Breeding Vertebrates. *Science*, 302(5645), 634 – 636.

Haag, L., 2007. Gibbons in the smoke: Experiences of a field study on Bornean white-bearded gibbons (*Hylobates albibarbis*) in central Kalimantan (Indonesia). *Gibbon Journal*, 3, 28-34.

Harlow, H.F., 1965. Total Social Isolation: Effects on Macaque Monkey Behaviour. *Science*, 148(3670), 666.

Harlow H.F, Dodsworth R.O, Harlow M.K., 1965. Total social isolation in monkeys. *Proceedings National Academy of Science*, 54, 90–97.

Hinde, R.A., 1975. The concept of function. In: Bearends, G., Beer, C. and Mannings, A., eds. *Function and evolution in behaviour*, Clarendon Press, Oxford, 3-15.

Hol, T., Van den Berg, C.L., Van Ree, J.M. and Spruijt B.M., 1999. Isolation during the play period in infancy decreases adult social interactions in rats. *Behavioural Brain Research*, 100, 91–97.

Hosey, G.R. and Skyner, L.J. 2007. Self-injurious behavior in zoo primates. *International Journal of Primatology*, 28, 1431–1437.

Joffe, T.H., 1997. Social pressures have selected for an extended juvenile period in primates. *Journal of Human Evolution*, 32(6), 593-605.

Lee P.C., 1984. Ecological Constraints on the Social Development of Vervet Monkeys. *Behaviour*, 91(4), 245-262

Leighton, D.R., 1987. Gibbons: Territoriality and monogamy. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham R.W. and Struhsaker, T. T., eds. *Primate Societies*, 135-145. University of Chicago Press, Chicago and London.

Lewis, K. N., 2000. A comparative study of primate play behaviour: implications for the study of cognition. *Folia Primatologica*, 71, 417-421.

Mallapur, A. and Choudhury, B. C. 2003. Behavioural Abnormalities in Captive Nonhuman Primates. *Journal of Applied Animal Welfare Science*, 6(4), 275–284

Marsh, C.W., 1981. Time budget of Tana river red colobus. *Folia Primatologica*, 35, 30-50.

Martin, P. and Caro, T.M., 1985. On the functions of play and its role in behavioural development. In: Rosenblatt, J.S., Beer, C., Busnel, M. and Slater, P.J.B., eds. *Advances in the study of behaviour*, 15. Academic press Inc., Florida, 59-103.

Martin, P. and Bateson, P., 2007. *Measuring behaviour: an introductory guide*, third edition. Cambridge University press, Cambridge.

Mitani, J.C., 1987a. Territoriality and monogamy among agile gibbons (*Hylobates agilis*). *Behavioral Ecology and Sociobiology*, 20, 265-269.

Mitani, J.C., 1990. Demography of Agile Gibbons (*Hylobates agilis*). *International Journal of Primatology*, 11(5), 411-424.

Mittermeier, R.A. and Cheney, D.L., 1987. Conservation of primates and their habitats. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. and Struhsaker, T.T., eds. *Primate Societies*. The University of Chicago Press, Chicago, 477-497.

Mootnick, A. R. and Baker, E., 1994. Masturbation in captive *Hylobates* (gibbons). *Zoo Biology*, 13, 345–353.

Morrogh-Bernard, H., 2003. *Behavioural ecology of orang-utan (*Pongo pygmaeus*) in a disturbed deep-peat swamp forest, Central Kalimantan, Indonesia*. University of Cambridge, Cambridge.

Morrogh-Bernard, H., Husson, S., Page, S.E. and Rieley, J.O., 2003. Population status of the Bornean orang-utan (*Pongo pygmaeus*) in the Sebangau peat swamp forest, Central Kalimantan, Indonesia. *Biological Conservation*, 110, 141-152.

Muller-Schwarze, D. , Stagge, B. and Muller-Schwarze, C. 1982. Play Behavior: Persistence, Decrease, and Energetic Compensation During Food Shortage in Deer Fawns. *Science*, 215(4528), 85-87

Nash, L.T, Fritz, J., Alford, P.A. and Brent, L., 1999. Variables influencing the origins of diverse abnormal behaviours in a large sample of captive chimpanzees (Pan troglodytes). *American Journal of Primatology*, 48(1), 15-29.

Nijman, V., 2005. Hanging in the Balance: An Assessment of trade in Orang-utans and Gibbons in Kalimantan, Indonesia. TRAFFIC, Southeast Asia, available at <http://www.traffic.org/mammals> (accessed on 01.11.08).

Nijman, V. and Menken. S.B.J., 2005. Assessment of census techniques for estimating density and biomass of gibbons (Primates: *Hylobatidae*). *The Raffles Bulletin of Zoology*, 53(1), 69-179.

Nijman, V., Richardson, M. and Geissmann, T., 2008. *Hylobates albibarbis*. In: *IUCN 2009. IUCN Red List of Threatened Species. Version 2009.1.* www.iucnredlist.org. Downloaded 01.09.2009

Orams, M.B., 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. *Tourism Management*, 23, 281–293.

Page, S.E., Rieley, J.O., Shotyk, Ø.W. and Weiss, D., 1999b. Interdependence of peat and vegetation in a tropical peat swamp forest. *Philosophical Transactions of the Royal Society of London*, B 354, 1885-1807.

Page, S.E., Siegert, F., Rieley, J.O., Boehm, H.V., Jaya, A. and Limin, S., 2002. The amount of carbon released from peat and forest fires in Indonesia during 1997. *Nature*, 420, 61-65.

Palagi, E., Cordoni, G., and Borgognini Tarli, S. M., 2004. Immediate and Delayed Benefits of Play Behaviour: New Evidence from Chimpanzees (Pan troglodytes). *Ethology*, 110, 949-962.

Palombit, R. A. 1994. Dynamic pair bonds in Hylobatids: implications regarding monogamous social systems. *Behaviour*, 128, 65-101.

Palombit, R. A. 1994. Extra pair copulations in a monogamous ape. *Animal Behaviour*, 47, 721-723.

Panksepp, J., 1981. The ontogeny of play in rats. *Developmental Psychobiology*, 14, 327-332.

Panksepp, J., Siviy, S. and Normansell, L., 1984. The psychobiology of play: theoretical and methodological perspectives. *Neuroscience and biobehaviour review*, 8(4), 465-92.

Pereira, M. E. and Preisser, M. C. 1998. Do Strong Primate Players 'Self-Handicap' during Competitive Social Play? *Folia Primatologica*, 69(3), 177-180.

- Poirier, F., 1969a. The Nilgiri langur troop: its composition, structure, function, and change. *Folia Primatologica*, 19, 20-47.
- Poirier, F., 1970. Nilgiri langur ecology and social behaviour. In Rosenblum, L.A., ed. *Primate behavior: developments in field and laboratory research*. Academic Press, New York, 251-383.
- Poirier, F.E. and Smith, E.O., 1974. Socialising Functions of Primate Play. *American Zoology*, 14, 275-287.
- Prince, P.A. and Francis, M.D., 1984. Activity Budgets of Foraging Gray-Headed Albatrosses. *The Condor*, 86(3), 297-300.
- Pusey, A.E and Packer, C., 1987. Dispersal and philopatry. *Behaviour*, 101, 275-310
- Raemaekers, J., 1979. Ecology of Sympatric Gibbons. *Folia Primatologica*, 31, 227-245
- Reichard, U. and Barelli, C., 2008. Life history and reproductive strategies of Khao Yai *Hylobates lar*: Implications for social evolution in apes. *International Journal of Primatology*, 29, 823-844.
- Reichard, U. and Sommer, V., 1997. Group encounters in wild gibbons (*Hylobates lar*): aginism, affiliation and the concept of infanticide. *Behaviour*, 134(15/16), 1135-1174.
- Reiley, J.O., Page, S.E., Limin, S.H. and Winarti, S., 1997. The peatland resource of Indonesia and the Kalimantan peat swamp forest research project. In Rieley, J.O. and Page, S.E. eds. *Tropical peatlands*. Samara Publishing Limited, Cardigan, 37-44.
- Rubenstein, D.I., 1978. On predation, competition, and the advantages of group living. *Perspective in Ethology*, 3, 205-31.
- Schultz, A., 1956. Postembryonic age changes. In: Hofer, H., Schultz, H. and Starck, D., eds. *Primatologia*. S. Karger, Basel, 887-964.
- Schultz, A., 1969. *The life of primates*. Weidenfeld and Nicolson, London.
- Shepherdson, D., Bement, N., Carman, M. and Reynolds, S., 2007. Auditory enrichment for Lar gibbons *Hylobates lar* at London Zoo. *International Zoo Yearbook*, 28:1, 256-260.
- Sommer, V. and Reichard, U., 2000. Rethinking monogamy: the gibbon case. In: Kappeler, P.M. ed. *Primate males: Causes and consequences of variation in group composition*. Cambridge press, England, 159-168.
- Spinka, M., Newberry, R.C. and Bekoff, M., 2001. Mammalian play: training for the unexpected. *The quarterly review of biology*, 76(2), 141-168.

Srikosamatara, S., 1984. Ecology of pileated gibbons in South-East Thailand. In: Preuschoft, H., Chivers, D., Brockelman, W.Y. and Creel, N., eds. *The lesser apes: Evolutionary and behavioural biology*. Edinburgh University Press, Edinburgh, 242-257.

Stockwell, C.A., Bateman, G.C. and Berger, J., 1991. Conflicts in national parks: A case study of helicopters and bighorn sheep time budgets at the Grand Canyon. *Biological Conservation*, 56(3), 317-328.

Suomi, S.J., 1997. Early determinants of behaviour: evidence from primate studies. *British Medical Bulletin*, 53(1), 170-184.

Sutherland, W. J., 1998. The importance of behavioural studies in conservation biology. *Animal Behaviour*, 56, 801-809.

Tenaza, R.R., 1975. Territory and Monogamy Among Kloss' Gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. *Folia Primatologica*, 24, 60-80.

Trivers, R.L., 1971. The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology*, 46(1).

Tsumori, A., 1967. Newly acquired behaviour and social interaction of Japanese monkeys. In: Altmann, S. A., ed., *Social communication among primates*. University Chicago Press, Chicago, 207-221.

UNEP-WCMC. 10 September, 2009. *UNEP-WCMC Species Database: CITES-Listed Species On the World Wide Web* : <http://www.unep-wcmc.org/isdb/CITES/Taxonomy/tax-species-result.cfm/isdb/CITES/Taxonomy/tax-species-result.cfm?displaylanguage=eng&Genus=%25hylobates%25&source=animals&Species=albibarbis&Country=>

Van Nieuwstadt, M.G.L. and Sheil, D., 2005. Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. *Journal of Ecology*, 93, 191–201.

Van Schaik, C.P. and Kappeler, P.M., 2003. The evolution of social monogamy in primates. In: Reichard, U.H and Boesch, C., eds. *Monogamy: Mating strategies and partnerships in birds, humans and other mammals*. Cambridge University Press, Cambridge, 59-80.

Whitten, A.J., 1984. Ecological comparisons between Kloss gibbons and other small gibbons. In: Preuschoft, H., Chivers, D., Brockelman, W.Y. and Creel, N., eds. *The lesser apes: Evolutionary and behavioural biology*. Edinburgh University Press, Edinburgh, 242-257.

Appendix 1: An example of the behavioural data sheet used for the study.

Tanggal							Awan		Angin	
Owa2							Hujan		Temp	
Obs										
Time	Aktivitas	Aktivitas 2	Initiator	Focus	Away from mum	Distance travelled/ jarak jalan	Height in tree/Owa2 ketinggian di pohon	Tree ht/ tinggi pohon	Nearest other gibbon	Notes/tanda
04:30										
04:35										
04:40										
04:45										
04:50										
04:55										
05:00										
05:05										
05:10										
05:15										
05:20										
05:25										
05:30										
05:35										
05:40										
05:45										
05:50										
05:55										
06:00										
06:05										
06:10										
06:15										
06:20										
06:25										
06:30										

Appendix 2: Qualitative data taken during and in between scan samples with explanatory codes

SAF	Sub-adult female	OU	Orang-utan (<i>Pongo pygmaeus</i>)
SAM	Sub-adult male	Klassi	Red langurs (<i>Presbytis rubicunda</i>)
JUV/JM	Juvenile male	P	Play
INF	Infant	CH	Chase
AF	Adult female	WR	Wrestle
AM	Adult male	GR	Grab
ALG	Allo-groom	PB	Play with branch

Female sub-adult of Group C (Cynthia)

08.56- Chasing, SAF initiator	10.57, SAF lying down, JM bats her with arm, play invitation	AF calling, SAF replies and moves towards her
08.59- Grabbing, SAF and JM	11.00 Adults mating, JM squeaking in protest and comes down tree and swings near them	SAF and JM chasing and grabbing climbing round the tree
09.04- Chasing SAF and JM	Adults still mating, JM still protesting but cannot be seen	JM and SAF feeding together, all in same tree
09.09- Wrestling SAF and JM	Quite far from AF	JM and SAF feeding together, all in same tree
09.21- Play chasing SAF and JM	Hanging Quite spread out as a family, 20M+ from AF	06.14- ALG, whilst hanging and swinging
09.37- Chasing SAF and JM	Towards AF, hanging and feeding	7.06- P-wr with JUV
07.44 JM and SAF wrestling in tree. Dewa thinks initiator JM and focus SAF but not 100% sure.	7.36 Red Langurs (Klassi) watching observer	All in same tree
SAF travelling at back of group	Langurs travelling with Group C	09.22-JUV grooms SAF's head
JM hanging in tree, SAF jumped onto tree and grabbed him	9.18- Play, hanging	9.27-P-wr with JUV
AF leading group	Travelling together, JM in front	09.43-P-wr with JUV
SAF initiates wrestling with JM, he responds and wrestles too; then cries	JM joined SAF and AF in tree	11.14- WO
And JM, 09.39 SAF chasing JM	Play, chasing JM chasing SAF	12.12-P-Cha with JUV

Female sub-adult of Group Karate (Zyang Zizi)

05.51-AF chased SAF away, physical contact	SAF came towards JUV and made him move away from his place	All family in same tree
Alert and watching	JUV in same tree feeding	All family in same tree
WO	6.09-P-HA upside down	All family in same tree
WO	6.17-INF squeaking and chasing SAF	All family in same tree
08.19 S-ALG	P-WR/CHA, JUV CHA SAF, wrestling lot more vigorous and physical and moving around more trees during chase than when playing with INF	hanging
Travelling low 6-10, S-ALG	Aggression from AM towards SAF, chased and bit on back	hanging
Male comes and hoots	Self-grooming	hanging 11:27h Wrestling
Feeding in same tree	P-CHA- JUV to SAF	hanging 11:28 grabbing and swinging
9.08, Fighting, hoots and squeaks, probably SAF and AM	Self-grooming	hanging 11:31 and 11:33 wrestling 11:36 grooming INF 11:37 SAF resting while INF plays around her 11:38 same as 11:37
S-ALG	SAF catching falling big brown leaves	11:41 INF leaves SAF
Came down to 1-5m	P-Cha, JUV to JUV	12:03 SAF grooming AM
06.29 S-ALG	Chasing	12:03 SAF grooming AM

Female sub-adult of Group Ninja (Nina)

Whole family in two trees, singing. Great calling with AF and SAM, 5 times	11.44-P-GR/WR with INF	SAF and INF chasing then wrestling/grabbing but then out of sight
6.38- Feeding at 1-5m	11.48-SAF grooming INF	10:37 INF, SAM and SAF all play chasing. INF in middle. Then just SAM and INF playing and wrestling with SAF sitting <1m away
P-CHA- SAM	08:47 SAF chasing SAM, much more vigorous than when with INF	10:44 SAM and INF wrestling and chasing >5m from SAF
08.27-SAF and AM grooming each other	09:16 SAF hoots	10:50-10:59 Neo and INF playing >10m from SAF. INF very vocal
08.37-P-PB-swinging on liana	09:30-09:37 INF crying a lot	

Male sub-adult of Group Ninja (Neo)

AF and AM 7.17-started singing again
AM and AF and INF, SAF in different tree
AM and AF and INF, SAF in different tree
AM and AF and INF, SAF in different tree

Male juvenile of Group C (Ceeka)

7.31 WO and displaying, hitting trunk with left hand, while watching observers	All resting in same tree	INF-cries JUV leaves tree and goes to INF, AF hoots as well INF and AF are in a Rambutan hutan tree
AF and INF travelling together, not with rest of family. AF-P-gr INF and mo and ha	All resting in same tree	09.56-OU nest, P-wr/Pb and INF
WO and alert	All resting in same tree	OU-nest
and INF. JUV P-gr/wr/ch with INF	All resting in same tree	Whole family
Sitting with SAF and INF	All resting in same tree	Whole family
AF and INF	All resting in same tree	Whole family
AF and INF	All resting in same tree	Whole family
AF and INF	Whole family in tree (Rambutan hutan)	10.28-P-Ha with INF
AF and INF	Whole family in tree (Rambutan hutan)	P-Ha with INF. In tree with Klassi, watching it eat 1-5m, SAF joins, Klassi leave
AF and INF	6.44-P-gr the INF	JUV chasing INF but INF initiated
Family feeding in same tree	P-WR/GR	P-Mo, INF in tree with JUV
Family feeding in same tree	7.01- 0-5M Came down to feed	Whole family
Family feeding in same tree	7.12-P-GR/Cha INF initiating	Fighting, AM leaves tree
All resting in same tree	7.17-Gr/Cha, 07.19-Cha	7.36-P-WR, SAF and JUV
All resting in same tree	7.23-Ha on JUV- JUV upsde dow, 07.23- WR-HA whilst wrestling	9.02 P-Cha, SAF and JUV, 8.03-self grooming
All resting in same tree	7.34-Gr-SAF, 7.35- Gr SAF, squabble over food?Cha and GR	09.01-P-Gr/ha with INF, INF Grabs JUV
All resting in same tree	07.53- INF-P-Cha/Gr/Wr	10.06-P-Cha/Gr, INF to JUV
All resting in same tree	Gr/cha/wr	10.16-P-WR/Cha with INF

Male juvenile of Group Karate (Jet Li)

7.31 WO and displaying, hitting trunk with left hand, while watching observers	All resting in same tree	INF-cries JUV leaves tree and goes to INF, AF hoots as well INF and AF are in a Rambutan hutan tree
AF and INF travelling together, not with rest of family. AF-P-gr INF and mo and ha	All resting in same tree	09.56-OU nest, P-wr/Pb and INF
WO and alert	All resting in same tree	OU-nest
and INF. JUV P-gr/wr/ch with INF	All resting in same tree	Whole family
Sitting with SAF and INF	All resting in same tree	Whole family
AF and INF	All resting in same tree	Whole family
AF and INF	All resting in same tree	Whole family
AF and INF	Whole family in tree (Rambutan hutan)	10.28-P-Ha with INF
AF and INF	Whole family in tree (Rambutan hutan)	P-Ha with INF. In tree with Klassi, watching it eat 1-5m, SAF joins, Klassi leave
AF and INF	6.44-P-gr the INF	JUV chasing INF but INF initiated
Family feeding in same tree	P-WR/GR	P-Mo, INF in tree with JUV
Family feeding in same tree	7.01- 0-5M Came down to feed	Whole family
Family feeding in same tree	7.12-P-GR/Cha INF initiating	Fighting, AM leaves tree
All resting in same tree	7.17-Gr/Cha, 07.19-Cha	7.36-P-WR, SAF and JUV
All resting in same tree	7.23-Ha on JUV- JUV upsde dow, 07.23- WR-HA whilst wrestling	9.02 P-Cha, SAF and JUV, 8.03-self grooming
All resting in same tree	7.34-Gr-SAF, 7.35- Gr SAF, squabble over food?Cha and GR	09.01-P-Gr/ha with INF, INF Grabs JUV
All resting in same tree	07.53- INF-P-Cha/Gr/Wr	10.06-P-Cha/Gr, INF to JUV
All resting in same tree	Gr/cha/wr	10.16-P-WR/Cha with INF

Female infant of Group Karate (Brandi)

Found at 9.08, watching observer	P-mo And Ha	7.44 Squeaking noises,
Possibly feeding	08.12 Infant P-Mo and Ha	07.47- INF P-Mo whilst AF feeding
Infant cried	Swinging around, then climbs down tree to AF	INF grooming AF
Feeding as family in a tree	8.48-8.57 CH with JUV, JUV/INF and AF all in same tree, AM in adjacent tree	08.21 chasing JUV
Feeding as family in a tree	Juvenile chasing Infant	drinking water, with AF
Feeding as family in a tree	AF feeding, Infant reaching out and grabbing her, she grabs back, they pull each	08.47 brachiating on own

	other	
Feeding as family in a tree	Infant chasing Juv, infant making hooting noises	Squeaking
Feeding as family in a tree	JUV chasing INF	INF also grabbing JUV
Infant hanging alone, mum reached out and pulled infant to her		AF feeding, she plucked leaves and the INF took
AF feeding, INF travelling with	AF feeding, Infant P-Mo around tree	11.37- WO
AF feeding, INF travelling with	HA and WR with JUV	12.21 AF with baby on, chasing SAF down tree
AF feeding, INF travelling with	10.17- On AF to travel, climbs off and P-Mo whilst she feeds	Jumping
AF feeding, INF travelling with	10.18- Swinging and trying to grab/get to AF	INF went back to AF for cuddle
AF feeding, INF travelling with	Also close to AM	INF attempts singing
Hanging and playing on Liana, away from AF, swinging, grabbing liana and moving around tree, within 8M	Playing on own, swinging toward AM and grabs AM, AM reciprocates and grabs and pulls back	05.16 INF tries singing again
10.57 Hanging upside down	10.53- family come together	05.58- INF attempts singing again
11.01, back in view, away from AF, swings towards her, she puts hand out to infant, infant has cuddle. 1102, climbing on own again	Infant making squeaking noises	6.03- feeding on AF
11.22, away from Mum, playing, ha, swinging and manipulating branches	Travelling	Returns to AF
11.43, Watching observer and hanging	Travelling	AF in next tree, had to return as INF crying
Multiple gibbons singing, infant crying	Travelling	Brachiating through tree
06.06 Infant Playing- Moving around tree away from AF	AF following INF	INF playing on own, moving round tree lots during AF feeding bouts
Travelled to next tree behind AF, not on her	JUV chasing INF	Travelled to AF on own
Infant travelled to next tree first	Travelling fast	INF feeding on own
Cl/m- M/T	Travelling fast	Hanging off AF upside down
Infant P-Mo around tree on own about 5m from AF	Travelling fast	Ch with JUV
7.14 INFANT P-MO	Travelling on AF, then comes off climbs around tree then climbs back towards AF	Came down 0-6 cl/mu
Infant WO	possibly feeding	Playing with JUV ch and gr
Infant Cl/Mu- M/T	possibly feeding	P with JUV cha and Gr
Moving quite a lot, rest of family spread out, with AF,	Playing on own in between, climbing around tree	Squeaking

AF feeding and occasionally giving some to Infant		
7.34 Infant P-Ha		

Male infant of Group Ninja (Nidji)

05.38, P-mo,ha. AF,SAM and SAF all feeding in tree with infant	INF and SAM playing in Orangutan nest	12.01- P-HA
5.44, animal followed by SAF and SAM. 5.48 INF jump, p-mo and p-ha	10.03- INF So-Gr AF	SA chasing klassi away
Next to AF, less than 2m	06.48 INF feeding alone	INF travelling to next tree on own
5.59 Inf jump and chase Hornbill, fighting over figs	P- with SA, INF gr SA	07.56-INF cried
SAM and SAF brachiate towards feline animal and follow, chasing it away from family SAM return from chasing animal	7.03 SA gr and cha with INF. 07.04-INF swinging nd hanging while eating	INF-P-Cha with SAM
6.10 Hooting into singing and great calls. Infant playing	07.09- wr/gr SA	SAM-autoplay, swung out to INF
Nidji trying to sing	07.17- P-GR SA, 07.18- gr/wr/ha	08.41-INF travelling alone, P-MO/GR AF
Nidji trying to sing	07.22, Travelling alone	08.45-INF threw stick at observer
Nidji trying to sing	7.23- INF crying	08.57-P-MO
Nidji trying to sing	08.38- P/HA/MO	P-CHA/GR/WR
Nidji trying to sing	08.42- Aggression from adult (female?) towards SA(male?) playing with infant too roughly?	P-CH/GR with SAM
Nidji trying to sing	08.54- INF Travelling alone, brachiating and walking, AF following	P-GR by AF
Nidji trying to sing	08.59- P-HA/MO	INF crossed tree on own, eating rambutan on own
Nidji trying to sing	09.23- P-MO	brachiated on own, 4 trees following SAM
P-GR SAM	P/R in orangutan nest	
06.36 Cha SAF	In orangutan nest	11.03-INF crying
06.49 AF leaves tree, INF squeals, AF returns carries to next tree	10.36- SA chase INF. 10.38- P-ha	INF- P-GR/MO/HA
07.06 INF P- SAM and SAF	10.41- INF crying	INF- P-GR/MO/HA
7.08 Adults mating, INF squealing and swinging towards them	INF came down tree and joined AF, AM and SAF	INF- P-GR/MO/HA
07.29 INF Brachiating alone	11.34- INF-allogrooming	INF- P-GR/MO/HA

08.01 INF crying	11.37- P-HA	P-WR/GR with SAM
Travelling with AF	11.59- WO	12.51-HA, upside down held by INF's foot by SAM, HA/WR with SAM
9.30- P- CH,WR,GR, HA		