

**Food Selection by
Northern Yellow-cheeked Crested
Gibbons (*Nomascus annamensis*) in
Northern Cambodia**

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Abstract

Tropical regions have extremely high plant diversity, which in turn supports a high diversity of animals. However, not all plant species are selected by animals as food sources, with some herbivores selecting only specific plants as food as not all plants have the same nutrient make up. Animals must select which food items to include in their diets, as the amount and type of nutrients in their diet can affect lifespan, health, fitness, and reproduction.

Gibbon populations have declined significantly in recent years due to habitat destruction and hunting. Northern yellow-cheeked crested gibbon (*Nomascus annamensis*) is a newly described species, and has a limited distribution restricted to Cambodia, Laos and Vietnam. The northern yellow-cheeked crested gibbons play an important role in seed dispersal, yet little is currently known about this species, including its food selection and nutritional needs. However, data on food selection and nutritional composition of selected food items would greatly inform the conservation of both wild and captive populations of this species.

This study aims to quantify food selection by the northern yellow-cheeked crested gibbons by investigating the main plant species consumed and the influence of the availability of food items on their selection. The study also explores the nutritional composition of food items consumed by this gibbon species and identifying key plant species that provide these significant nutrients.

A habituated group of the northern yellow-cheeked crested gibbons with five members located in northern Cambodia was studied for 12 weeks during the dry season, and focal animal sampling was used to observe individual feeding behaviours. Four main activity categories were recorded including resting, feeding, travelling and socializing. Phenological data was recorded from transect lines, and plant densities from 20 vegetation plots inside the home range of this group of gibbons were also measured. Seventy-four plant samples from 20 tree and liana species that were consumed by this group of gibbons were collected for nutritional analyses. These samples were initially dried in sunlight, and then oven dried before levels of protein, total non-structural carbohydrates, lipids, fibres and condensed tannins were measured at the Nutritional Ecology Lab at Hunter College of the City University of New York, New York.

The northern yellow-cheeked crested gibbon individuals spent most of the time resting, followed by feeding, travelling and socializing. Their main diet was fruit, supplemented with young leaves, flowers, mature leaves, and occasionally insects. Individuals selected food from 37 plant species, but predominately fed on just 16 of these species. The three most-consumed species were fruit from *Ilex umbellulata* (tree), *Ficus. sp* (liana), and young leaves from *Lithocarpus elegans* (tree). There was a significant relationship between feeding time and the availability of flowers, indicating that flowers were actively selected for when present. However, there was no significant relationship between feeding time and the availability of fruit or young leaves. Only a small number of plants bore fruit, with very low densities in the home range of this gibbon study group, but these plants produced a large abundance of fruit. These findings clearly indicate that fruit is the main diet for northern yellow-cheeked crested gibbons in the dry season, with young leaves, flowers, mature leaves and insects acting as secondary food sources. The northern yellow-cheeked crested gibbons selected only a small number of specific plants in their territory for food sources, indicating that any selective logging targeting these plant species would reduce food availability, and restrict the diet of these animals.

Fruits consumed by the northern yellow-cheeked crested gibbons were rich in carbohydrates and lipids, while young leaves were richest concentration of protein. Mature leaves had a high moisture content, whereas flowers contained condensed tannins more often than other plant tissues. All plant tissues consumed had similar amount of fibres. Generally, the food items consumed had higher concentrations of carbohydrate than protein or lipids. The overall diet of this group of gibbons was low in lipids. These results indicate that northern yellow-cheeked crested gibbon consumed food items with high concentrations of carbohydrate, and only selected a few food sources with high level of protein.

Overall, these findings have contributed important knowledge that can be used for long-term conservation of this gibbon species. There are a small number of key food species in the home range which need special protection. The northern yellow-cheeked crested gibbons consumed food items from different plant species, and as a consequence, all plant species selected play an important role for nutritional requirements by this gibbon species. When considering feeding requirement by the northern yellow-cheeked crested gibbons for captive breeding programs, diets should include fruit, which is rich in carbohydrates, and young leaves, which have high levels of protein.

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List of Abbreviations

ADB	Asian Development Bank
ADF	Acid Detergent Fibre
ADL	Acid Detergent Lignin
ASEAN	Association of Southeast Asian Nations
CI	Conservation International
CITES	Convention on International Trade in Endangered Species
DBH	Diameter at Breast Height
FA	Forestry Administration
FAO	Food and Agriculture Organization
FAI	Food Availability Index
GPS	Global Position System
ICEM	International Centre for Environmental Management
ITTO	International Tropical Timber Association
IUCN	International Union for the Conservation of Nature
L	Lipids
Laos PDR	Laos' People Democratic Republic
NDF	Neutral Detergent Fibre
NGOs	Non-Governmental Organizations
NRC	National Research Council
ODC	Open Development Cambodia
P	Protein
PAF	Primate Action Fund
PCI	Primate Conservation Incorporated
RMT	Right-angled Mixture Triangle
SSC	Species Survival Commission
TNC	Total non-structural carbohydrates
UNDP	United Nation Development Program
VSSPCA	Veun Sai-Siem Pang Conservation Area
WCS	Wildlife Conservation Society

Chapter 1

General introduction

1.1 Global threat to wildlife populations

1.1.1 Extinction risks for wild animals

Global wildlife populations have declined at an alarming rate in the last few decades (Pimm & Raven 2000; Schipper *et al.* 2008). Twenty-five percent of all mammalian species whose status have been recorded are faced with extinction, while other species have already gone extinct (Brooks *et al.* 2002; Galbreath *et al.* 2006; Schipper *et al.* 2008). The highest declines in global wildlife populations have been from areas of high species richness such as biodiversity hotspots in Southeast Asia and Africa (Ceballos & Ehrlich 2002; Schipper *et al.* 2008; Duckworth *et al.* 2012). Terrestrial mammals in South and Southeast Asia face a higher extinction risk compared to other regions (Schipper *et al.* 2008; Duckworth *et al.* 2012) and Ceballos and Ehrlich (2002) argue that the extinction rate of mammals in Southeast Asia is between 75 and 100%. This is primarily due to anthropogenic pressures, such as deforestation, land use changes and hunting (Brook *et al.* 2003; Nakamura *et al.* 2014; Sharma *et al.* 2014). For example, due to anthropogenic pressure, both Pere David's deer (*Elaphurus davidianus*) native to the subtropics of China (Ceballos & Ehrlich 2002) and the Vietnamese sika deer (*Cervus nippon pseudaxis*) (Thévenon *et al.* 2003) are now extinct in the wild. The extinction of these species signals serious threats to global biodiversity (Ceballos & Ehrlich 2002). Without conservation and research efforts, and the reduction of pressure on wildlife and their habitats, other species listed as Critically Endangered or Endangered by the International Union for the Conservation of Nature (IUCN) Red List as well as species with small geographical ranges will probably go extinct in the near future (Ceballos *et al.* 2005; Schipper *et al.* 2008).

1.1.1.1 Decline in wildlife populations in Cambodia

Cambodian wildlife populations have declined significantly from 1953 to 2005, with the most rapid period of decline occurring during the 1970s (Loucks *et al.* 2009), and with a continued decline in the last few decades (Walston *et al.* 2010; O'Kelly 2013). Armed conflict and civil war were the root of these declines, particularly during the Lon Nol (1970-1975) and Pol Pot (1975-1979) regimes (Loucks *et al.* 2009; Gray *et al.* 2012). Hunting with

machine guns, increasingly available after the conflicts, and internal and external wildlife trade were the main reasons for declining wildlife populations in Cambodia (Loucks *et al.* 2009). Large mammals including tigers (*Panthera tigris*), leopards (*Panthera pardus*), Asian elephants (*Elephas maximus*), wild cattle (gaur *Bos gaurus*, banteng *Bos javanicus*, kouprey *Bos sauveli*, and wild water buffalos *Bubalus arnee*), eld's deer (*Rucervus eldii*) and hog deer (*Hyelaphus porcinus*) were the most targeted species during these periods (Gray *et al.* 2012). These hunting pressures might have driven at least one species, the kouprey (*B. sauveli*), which is the Cambodian national mammal, to extinction in the past few decades (Galbreath *et al.* 2006; Hassanin *et al.* 2006). Tigers are also likely to become extinct in most regions in Cambodia, due to similar pressures (Walston *et al.* 2010; O'Kelly *et al.* 2012). Tigers were confirmed to be present in some important areas in 2001 (Lynam 2010). However, since 2005, camera trap surveys have not recorded tigers in the Virachey National Park (Walston *et al.* 2010), and only a single photograph has been recorded in Cardamom Mountain (Lynam 2010).

Due to poverty and the demand for basic food resources, Cambodian wildlife provides a source of protein and traditional medicine for local people who live near wildlife habitats (Hon *et al.* 2010; Starr *et al.* 2010; Starr *et al.* 2011; Alves *et al.* 2013; Clements *et al.* 2013a). Wild animals are being hunted not only for personal consumption, but also to sell at local markets (Hon *et al.* 2010; Starr *et al.* 2010), particularly in remote provinces. Asian small-clawed otters (*Aonyx cinerea*) and smooth-coated otters (*Lutrogale perspicillata*) are hunted in the remote areas of northern Cambodia for meat, and skins are sold for traditional medicine at local markets (Hon *et al.* 2010). Similarly, one of the rarest primates in Cambodia, pygmy slow lorises (*Nycticebus pygmaeus*) are hunted by local people for traditional medicine (Starr *et al.* 2011). The impacts of these activities can be seen on the IUCN Red List, which lists 45 mammals (seven Critically Endangered or Endangered), 17 reptiles (nine Critically Endangered or Endangered), and 46 birds (12 Critically Endangered or Endangered) in Cambodia (WCS 2009; Clements *et al.* 2010).

1.2 Global deforestation

Habitat loss through deforestation and degradation are the main threats to mammals worldwide (Pimm & Raven 2000; Brooks *et al.* 2002; Nakamura *et al.* 2014), and this particularly affects Asia, the Americas, and Africa (Schipper *et al.* 2008). Globally, 5.2 million hectares of tropical forests lost per year (FAO 2010). Fewer than 5% of tropical forests are protected around the world, and even these protected forests are often illegally exploited (Chapman *et al.* 2000). In addition, 403 million hectares of tropical forests were recently proposed for selective logging (Putz *et al.* 2012). Moreover, a vast majority of felled forests are cleared and transformed into agricultural areas (Bender *et al.* 1998; Oates *et al.* 2000), including cattle farms in Brazil (Malhi *et al.* 2008), rubber plantations in China (Li *et al.* 2007), tea and coffee farms in Sri Lanka (Wickramagamage 1998), pine plantations (Cheyne *et al.* 2008) and palm oil plantations in Malaysia and Indonesia (Fargione *et al.* 2008). Globally, Brazil and Indonesia have the highest levels of forest cover loss, and Brazil has had a huge decline in forest loss in the last few years (Harris *et al.* 2012; Hansen *et al.* 2013). Table 1.1 shows the global forest cover loss between 2000 and 2012 (Hansen *et al.* 2013). The annual forest loss in Brazil was 40,000 km².year⁻¹ between 2003 and 2004, but declined to 20,000 km².year⁻¹ in 2010 to 2011, while in Indonesia it was 10,000 km².year⁻¹ between 2003 and 2004, and increased to 20,000 km².year⁻¹ from 2011 to 2012 (Hansen *et al.* 2013).

Table 1.1: Global forest cover lost between 2000 and 2012.

Regions	Forest types	Forest cover loss Km ² .year ⁻¹
Eurasia	Tropical rainforests	1393
Africa	Tropical moist deciduous forests	536
South America	Dry tropical forests	459
Eurasia	Tropical moist deciduous forests	221
Eurasia	Tropical dry forests	123

Source: Hansen *et al.* (2013)

1.2.1 Deforestation in Cambodia

The natural forest resources in Cambodia have been exploited since the late 1980s, starting at the end of the civil war in 1979 (Le Billon 2002). Forest cover in Cambodia was estimated at approximately 60% in 1991 and 55.7% in 1995, as recorded by the Food and Agriculture Organization (FAO)/United Nation Development Program (UNDP) (Lang 2001; Le Billon 2002). Logging was particularly high during the 1980s and 1990s, with large quantities of timber exported to neighbouring countries including Thailand and Vietnam (Le Billon 2000, 2002). Table 1.2 shows the volume of timber export (thousands m³) and the estimate value (millions \$USD) of those timbers in the 1990s (Le Billon 2000). The Cambodian timber export increased dramatically from 1990 to 1994, and gradually declined from 1995 until 2003 (Figure 1.1) (Le Billon 2000; ITTO 2003; Barney 2005). Consequently, Cambodia has lost approximately 29% of its forest cover, which is the highest rate of deforestation in mainland Southeast Asia (Cambodia, Laos and Vietnam) (Avtar *et al.* 2012), with an annual deforestation rate of 0.7% between 1973 and 2003 (Sasaki 2006) and 1.2% per year between 2005 and 2010 (Lambrick *et al.* 2014). Figure 1.2 demonstrates the latest updated trends in Cambodian forest cover between 1973 and 2014 (ODC 2014a).

Table 1.2: Volume (thousand m³) and value (millions USD) of Cambodian timber exports and government revenue (millions USD) from these exports between 1990 and 1998

	1990	1991	1992	1993	1994	1995	1996	1997	1998
Volume of timber exports (thousand m ³)	515	848	1,393	1,360	1,495	1,691	992	1,045	1,090
Estimated value (US\$ million)	77	170	348	340	374	423	248	188	218
Forestry government revenue (US\$ million)	n.a.*	n.a.*	1.5	3.3	39	27	11	12	5

Original reports from the Royal Government of Cambodia, Thai Forestry Department, and Global Witness. n.a.* = no available data.

Source: Le Billon (2000)

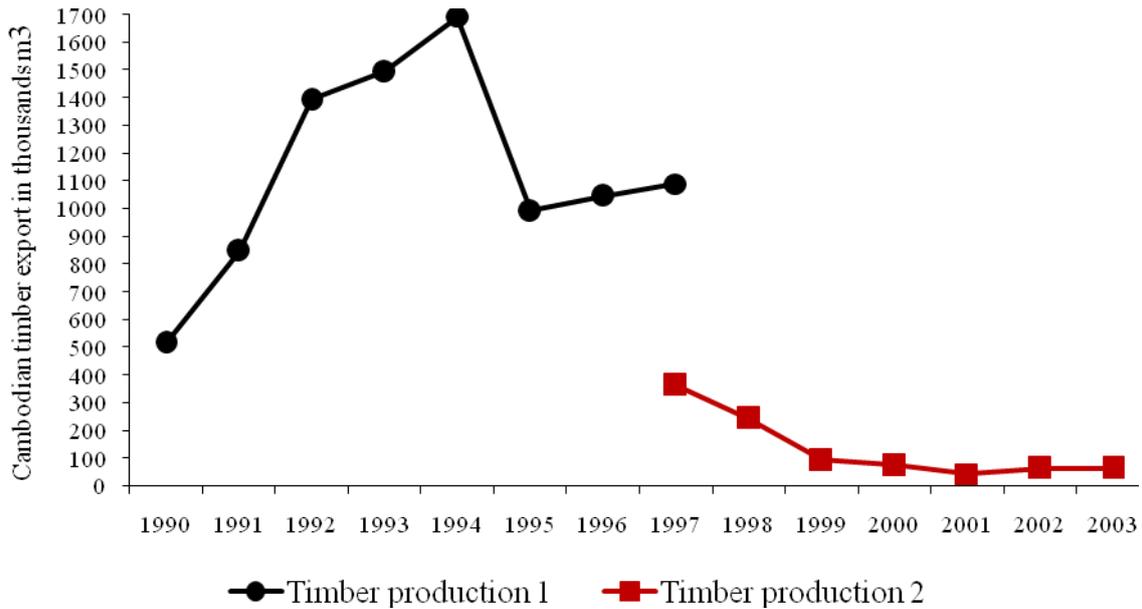


Figure 1.1: Cambodian timber exports (thousands m³) from 1990 to 2003. Timber production 1 (circle symbols) indicates the volume of timber export from 1990 to 1997 [original data from the Royal Government of Cambodia, Thai Forestry Department, and Global Witness, cited in Le Billon (2000)]. Timber production 2 (square symbols) indicates the total export timbers including logs, tropical sawnwood, veneer, and plywood from 1997 until 2003 [original source data from ITTO (2003) cited in Barney (2005)].

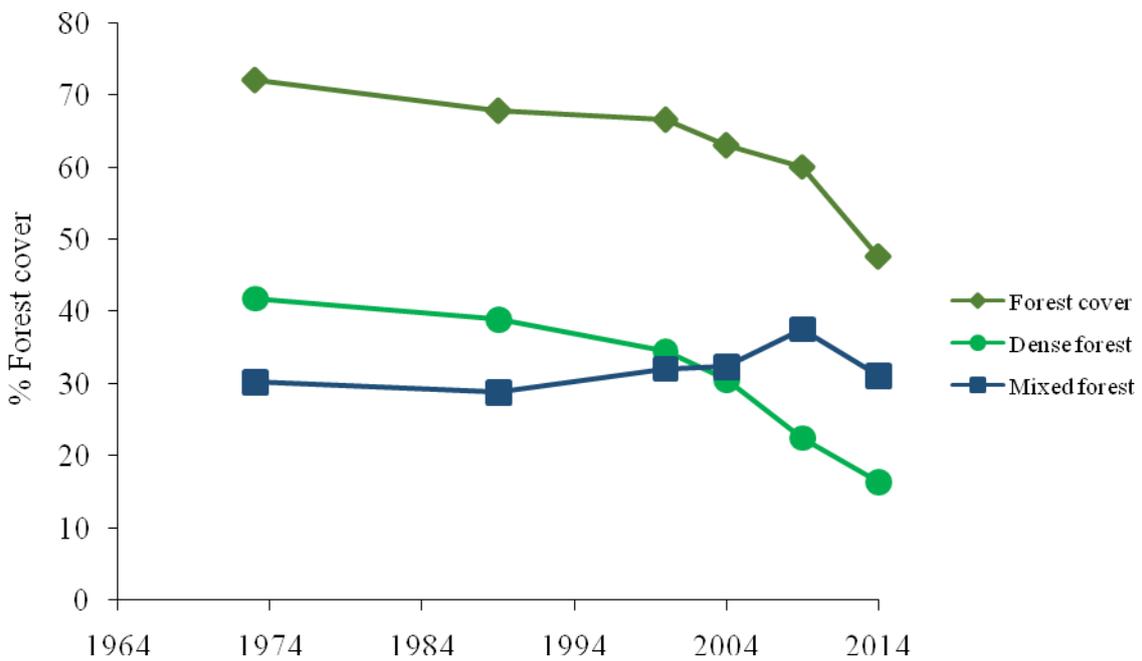


Figure 1.2: Cambodian Forest Cover from 1973 to 2014. Forest cover (diamond symbols) is the total tree canopy, and a combination of dense and mixed forest. Dense forests (circle symbols) are defined as evergreen and semi-evergreen forests. Mixed forests (square symbols) mainly refer to mixed deciduous forests, but these also include regrowth forests, mangrove forests, inundated forests, stunted forests, bamboo, and forest plantations, which include rubbers, acacia, eucalyptus or other tree crops.

Source: Open Development Cambodia (2014a).

1.3 Conservation in Cambodia

Since wildlife populations, including primates, have declined significantly, the Cambodian government has cooperated with international non-governmental organizations (NGOs) to protect and increase species-specific research. Because of this strong commitment, Cambodia has developed at least 23 protected areas including seven national parks, 10 wildlife sanctuaries, three landscape protected areas, and three multi-purpose areas (ICEM 2003; ODC 2014b), which is about 18% of the total land area (ODC 2014b). Such initiatives are needed to increase wildlife conservation in Cambodia. Cambodia has enacted many programs designed to protect key species. For example, the Cambodian national bird, the giant ibis (*Thaumatibis gigantea*), declined to less than 250 individuals in 1997 (Keo *et al.* 2009), but due to conservation efforts (Clements *et al.* 2010; Clements *et al.* 2013b), its population is now estimated at 345 individuals (BirdLife-International 2015).

Despite these conservation efforts, the challenges of conservation in Cambodia remain undeniable. The two main factors that lead to challenges to conservation in Cambodia are poverty (ADB 2014) and poor law enforcement (Clements *et al.* 2010). Cambodia is one of the poorest nations in Association of Southeast Asian Nations (ASEAN), with the vast majority of people rely on natural resources for their livelihoods, and most living under the poverty line (ADB 2014), leading to illegal activities occurring even in protected areas. Shifting cultivation is still being practiced, which adds to conservation concerns as it disrupts forest habitats (Baird & Dearden 2003). Although Cambodia has forestry, fisheries, and environmental laws, there are still weaknesses in putting this legislation into practice (De Lopez 2002; McKenney *et al.* 2004; Ratner 2006; Clements *et al.* 2010). There is not enough financial support to ensure adequate protection of natural resources by law enforcement teams, necessitating funding for biodiversity conservation by international NGOs (Milne & Niesten 2009; Clements *et al.* 2010; Clements *et al.* 2013b). However, the cost of setting up these areas and ensuring their protection is such that it is likely to be only a short-term solution, and external financial contributions are unlikely to be feasible long-term (Clements *et al.* 2010).

1.4 Threats to primates

Non-human primates are distributed mainly in Asia, Africa, and South and Central America (Mittermeier 1986; Cowlshaw & Dunbar 2000). For all the reasons described above, along with global warming, primate populations in all regions have significantly

declined in the last few decades (Wiederholt & Post 2010). Habitat destruction has received particular attention, as removing trees from inside the range of primates can negatively affect population size and reduce the overall food supply (Chapman & Onderdonk 1998). For example, the population size of the olive baboon (*Papio anubis*) and common chimpanzee (*Pan troglodytes*) in Uganda were lower in logged forested areas than non-logged forested areas (Plumptre & Reynolds 1994). Similarly, the population size of the Ugandan red colobus monkey (*Piliocolobus tephrosceles*) decreased as forest fragmentation increased (Chapman *et al.* 2006), which may be, in part, due to selective logging (Chapman *et al.* 2000). Food scarcity caused by logging forces primates to consume food of lower nutritional value, leading to the overall consumption of lower quality diets, which in turn can lower milk production by lactating females (Altmann *et al.* 1977). The reduced food supply that results from logging may also modify the ecological behaviour and activity budgets of primates (Johns 1986). For example, when food tree density is low, primates must spend comparatively more time travelling or searching for food, and less time resting (Hardus *et al.* 2012). This was seen following El Niño events that reduced food availability, in a population of spider monkeys (*Ateles. spp*) and woolly monkeys (*Lagothrix. spp*), both of which declined as a result (Wiederholt & Post 2010). It is clear that reduction of food availability affects lifespans of primates (Mattison *et al.* 2012) and reproductive success (Thompson & Wrangham 2008). Due to the pressures described above, the Miss Waldron's red colobus monkey (*Piliocolobus badius*) is probably extinct in Ghana (Oates *et al.* 2000).

Primate populations have also declined significantly due to wildlife trade for biomedical experimentation (Maldonado *et al.* 2009; Shepherd 2010). During the late 1960s and early 1970s, demand for primates for research by the biomedical and pharmaceutical industries was particularly high, and India and Peru exported approximately 20,000 to 50,000 primates per annum (Nijman *et al.* 2011). Similarly, between 2007 and 2008, 4,000 night-monkeys (*Aotus. sp*) were illegally traded in Brazil, Colombia and Peru for use in biomedical laboratories (Maldonado *et al.* 2009). The United States of America is the highest importer of primates for biomedical research (26%), followed by Japan (14%) and China (13%) (Nijman *et al.* 2011). These exports involved both legal and illegal trade across primate habitat countries (Shepherd 2010). Figure 1.3 shows the export of primates for biomedical research and other purposes, involving both captive and wild-caught animals (Nijman *et al.* 2011). Indonesia is a member of the Convention on International Trade in Endangered Species (CITES), but the international trade includes not only the legally

exported long-tailed macaque (*Macaca fascicularis*), but also the highly endangered primates listed in CITES Appendix I, which need the highest level of protection (Shepherd 2010). These include orang-utans (*Pongo. spp*) and gibbons (*Hylobates. spp*), the majority of which were caught in the wild (Nijman & Asia 2009; Shepherd 2010). The export of these wild-captured, highly endangered individuals would have been particularly damaging for local

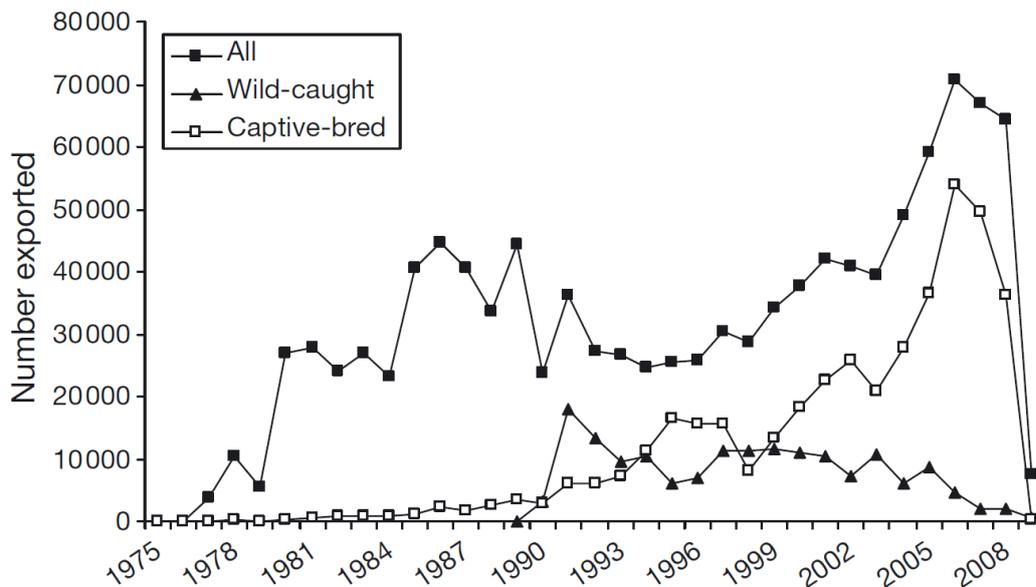


Figure 1.3: Export of wild caught and captive-breeding primates as reported by exporting parties to the CITES secretariat. The total export amounts to 1.1 million live individuals. In many years, the total number of animals actually exported is higher than the numbers wild caught or captive animals that were report as being exported to CITES.

Source: Nijman *et al.* (2011).

1.4.1 Cambodian primates

Knowledge of the distribution, abundance and status of Cambodian wildlife is limited (Coudrat *et al.* 2011), although at least 12 species of primates are found across the country (Table 1.3) (Rawson & Roos 2008; Nadler *et al.* 2010). However, like other primates around the world, Cambodian primates are now under threat (Nadler *et al.* 2010) (Table 1.3). Illegal logging, deforestation, agricultural development, hunting, illegal trade, mine development, and poor law enforcement all contribute to declining primate populations (Coudrat *et al.* 2011; Starr *et al.* 2011). Cambodian Primates are among the most poorly studied wild animals in Cambodia, with only a few species having been studied, such as the genera *Nomascus* (Frechette 2014; Nelson 2014; Frechette *et al.* in prep), *Nycticebus*, and *Hylobates* (Konrad 2004; Traeholt *et al.* 2006; Rawson & Roos 2008; Coudrat *et al.* 2011; Starr *et al.* 2011).

Table 1.3: Cambodian primates and their conservation status

N ^o	Family	Common name	Genus and species	IUCN status	Main threats	Sources
Hylobatidae						
1		Yellow-cheeked crested gibbon	<i>Nomascus gabriellae</i>	Endangered	Habitat loss, hunting, and illegal trade	(Geissmann <i>et al.</i> 2008)
2		Northern yellow-cheeked crested gibbon	<i>Nomascus annamensis</i>	Not assessed, but data suggest Endangered	Habitat lost, hunting, and illegal trade	(Long <i>et al.</i> 2011)
3		Pileated gibbon	<i>Hylobates pileatus</i>	Endangered	Habitat loss, hunting, and illegal trade	(Brockelman <i>et al.</i> 2008)
Cercopithecidae						
4		Black-shanked douc langur	<i>Pygathrix nigripes</i>	Endangered	Hunting, habitat loss	(Rawson <i>et al.</i> 2008)
5		Red-shanked douc langur	<i>Pygathrix nemaus</i>	Endangered	Hunting, habitat loss	(Ngoc Thanh <i>et al.</i> 2008)
6		Indochinese silvered langur	<i>Trachypithecus germaini</i>	Endangered	Hunting, habitat loss	(Nadler <i>et al.</i> 2008)
7		Assamese silvered langur	<i>Trachypithecus margarita</i>	Endangered	Habitat lost, hunting	(Nadler <i>et al.</i> 2010)
8		Pig-tailed macaque	<i>Macaca leonina</i>	Vulnerable	Illegal trade (pet), hunting	(Boonratana <i>et al.</i> 2008)
9		Stump-tailed macaque	<i>Macaca arctoides</i>	Vulnerable	Illegal trade (pet), hunting	(Htun <i>et al.</i> 2008)
10		Long-tailed macaque	<i>Macaca fascicularis</i>	Least concern	Illegal trade (pet), hunting	(Ong & Richardson 2008)
Lorisidae						
11		Pygmy slow loris	<i>Nycticebus pygmaeus</i>	Vulnerable	Hunting, illegal trade, habitat loss	(Streicher <i>et al.</i> 2008a)
12		Bengal slow loris	<i>Nycticebus bengalensis</i>	Vulnerable	Hunting, illegal trade, habitat loss	(Streicher <i>et al.</i> 2008b)

1.5 Primates and ecosystem services

Fruit eating primates play very important roles in maintaining ecosystems in tropical forests through seed dispersal and seed germination (Garber 1986; Chapman 1989; Stevenson 2000; Frechette 2014). They consume large quantities of fruit, and defecate or spit most of the seeds in areas where those seeds can survive, avoiding seed predators and distancing seeds from the shade and competition of their parent (Chapman & Onderdonk 1998). For example, more than 98% of chimpanzee dung (*Pan troglodytes*) in Kibale National Park, Uganda contained seeds, sometimes larger than 2 mm, suggesting they could disperse approximately 350 large seeds per km.day⁻¹ (Wrangham *et al.* 1994). There is a strong relationship between primate seed dispersal and plant distributions (Russo *et al.* 2005). Some plant species produce large seeds, which would be difficult to disperse by other agents beside primates (Russo *et al.* 2005; Nuñez-Iturri & Howe 2007). For example, the large seed of *Virola. spp* in Panama can only be dispersed by spider monkeys (*Ateles. spp*) (Russo *et al.* 2005). A study on seed dispersal by gibbons in northern Cambodia revealed that northern yellow-cheeked crested gibbons (*Nomascus annamensis*) play an important role in long distance seed dispersal (Frechette 2014). Germination of seeds dispersed by the genus *Alouatta* and *Lagothrix* is higher than seed germination without primate assistance, indicating that primate digestion improves seed germination (Stevenson *et al.* 2002). Consequently, any decline in primate populations may reduce seed dispersal that may in turn alter forest compositions (Nuñez-Iturri & Howe 2007).

1.6 Diet composition of primates

The dietary and nutritional requirements of non-human primates are very complex and variable among species (Chivers 1998; Strier 2007; Felton *et al.* 2009a). Primates are found in a diverse range of tropical forest habitats, their diets being primarily tree exudates (gummivory) (Yepez *et al.* 2005), leaves (folivory) (Davies *et al.* 1988; Kool 1992; Smith *et al.* 2013; Hanya & Bernard 2015), fruit (frugivory) (Whittington & Treesucon 1991; Laska *et al.* 2000; Fan *et al.* 2009) and/or insects (insectivory) (Goodall 1986; Fan *et al.* 2009). Different regions inhabited by primates provide particular food sources, and primates have evolved specific morphologies to exploit this diverse range of food sources (Strier 2007). Frugivores have a comparatively long small intestines, folivores have a

shorter intestine and some have a sacculated stomachs, gummivores have a proportionally long caecum, and insectivores have a short gut (Strier 2007).

Fruit or leaves alone are unlikely to meet all nutritional requirements of an animal (Chivers 1998) and very few species of plants, with some exceptions (e.g. figs), bear fruit all year round and instead produce fruit, leaves and flowers in a distinct seasonal pattern, with availability varying by season (Hamilton & Galdikas 1994; Wendeln *et al.* 2000; Hanya & Bernard 2012). Fruit production may also vary widely over time: for example, between 1998 and 2000, fruit production in Borneo was very low, with only a few tree species fruiting each month, and only one peak season in September 1998 (Te Wong *et al.* 2005). In contrast, fruit production in the same location was high between 2004 and 2008, with more than 98% of trees bearing fruit (Hanya & Bernard 2012). Primates need to be able to shift their diets from fruit to young leaves, mature leaves, flowers, or insects from season to season or year to year to meet their nutritional requirements when favoured food sources become scarce (Fan *et al.* 2009; Behie & Pavelka 2012a; Hanya & Bernard 2012).

Different parts of plants (fruit, leaves, flowers and seeds) contain a variety of nutrients, both favoured (proteins, carbohydrates, and lipids) and less favoured (fibres, tannins and alkaloids) by primates (Hamilton & Galdikas 1994; Rothman *et al.* 2006; Behie & Pavelka 2012a; Hanya & Bernard 2012, 2015). Consequently, every potential food item is a medley of favourable and unfavourable compounds, in varying combinations (Barton & Whiten 1994). It has been suggested that during a peak season of food availability, primates should favour high quality diets (easily digested, rich in protein and/or sugar) over poor quality diets that are difficult to digest (Strier 2007; Rothman *et al.* 2011). The Colobinae select food with higher protein and lower fibre content (Simmen *et al.* 2013), which leads to them ingesting mainly young leaves and seeds (Davies *et al.* 1988; Kool 1992) while avoiding mature leaves, which are more difficult to digest as they contain more fibre and secondary compounds (Davies *et al.* 1988). On the other hand, black howler monkeys (*Alouatta pigra*) select mature leaves over young leaves due to their high concentration of sugar, however, this selection may be due to the fact that this was found following a hurricane, which wiped out the majority of preferred food sources (Behie & Pavelka 2012a). This suggests that primate food preferences are highly dependent on species, environment (Smith *et al.* 2013) and morphology (Strier 2007).

Our knowledge of what drives food selection in wild and captive primates is limited to relatively few studies (Milton 1979; Rothman *et al.* 2006; Rothman *et al.* 2008b; Felton *et al.* 2009a; Felton *et al.* 2009c; Rothman *et al.* 2011; Behie & Pavelka 2012b; Simmen *et al.* 2013), yet this information is necessary to understand how best to preserve key food resources for wild populations and to ensure the best long-term care is given to captive populations and rehabilitation programs. For example, several studies show that figs play a very important role in maintaining food balance for many species of gibbons and monkeys (Wendeln *et al.* 2000; Serio-Silva *et al.* 2002; Felton *et al.* 2009c). Figs are a common food source in spider monkey habitats, as some species bear fruit for 8 to 9 months of the year (Felton *et al.* 2008). But, as the nutritional content of figs differs between species, they may provide different benefits (Serio-Silva *et al.* 2002). Some species contain high levels of inorganic materials (Felton *et al.* 2009c), while others are a rich source of calcium (Duhan *et al.* 1992; Behie & Pavelka 2012a), or have high levels of protein and low levels of fibre (Wendeln *et al.* 2000). This information is necessary to inform conservation programs to increase the protection of fig species. Although fig species are not commercially valuable, they play a crucial role in food security for primates and other wildlife (Duhan *et al.* 1992).

Many studies on food selection by primates suggest that nutritional composition of plant tissues (mainly protein) influences food selection (Davies *et al.* 1988; Kool 1992; Koenig *et al.* 1997; Behie & Pavelka 2012a; Smith *et al.* 2013), and food selection in turn influences health (Givens & Shingfield 2004), lifespan (Fernandes *et al.* 1976; Grandison *et al.* 2009; Trepanowski *et al.* 2011), social relationships, fitness, and reproduction (Koenig *et al.* 1997; Harris *et al.* 2010). For example, consuming low-protein diets can potentially increase the mortality rate of juvenile primates (Altmann *et al.* 1977), and caloric restrictions can have a negative effect on a lifespan of the normally long-lived rhesus monkeys (*Macaca mulatta*) (Mattison *et al.* 2012). In cases where food is available and of high quality, there is a positive correlation in chimpanzees between birth rates and the availability and quality of food sources (Thompson & Wrangham 2008). Savannah baboons (*Papio cynocephalus*) shows a positive correlation between food selection and population growth rates (Altmann & Alberts 2005). This suggests that both the quality and availability of food sources (Strier 2007; Felton *et al.* 2009b; Felton *et al.* 2009c) may influence food selection by primates (McConkey *et al.* 2002; Serio-Silva *et al.* 2002).

The consumption of a variety of food items by primate species may be representative of their attempt to target specific nutritional goals to survive (Felton *et al.* 2009a). Felton *et al.* (2009a) and others (Schoener 1971; Freeland & Janzen 1974; Milton 1979; Mattson 1980; Raubenheimer & Simpson 2004) propose five main models for primate nutritional goals: (i) maximising nitrogen (protein), (ii) maximising energy, (iii) limiting fibre content, (iv) avoiding secondary compounds and (v) balancing nutritional values.

Protein is one of the most important nutrients for primates (Milton 1979; Rothman *et al.* 2008b; Felton *et al.* 2009a; Rothman *et al.* 2011; Hanya & Bernard 2015), even though it may be consumed in low quantities by some primate species (Felton *et al.* 2009b). This is because a lack of nitrogen in the form of amino acids can affect health, reproduction, growth, and survival rates (Mattson 1980; Yiming 2006; Felton *et al.* 2009a; Felton *et al.* 2009b). As a consequence, some primate species need to maintain a minimum daily intake of protein, while allowing the relative proportion of other nutritional components in their diet to fluctuate, indicating that they select items based on protein contents that can help them reach their minimum requirement (Felton *et al.* 2009b).

The idea of energy maximization originated from optimal foraging theory (MacArthur & Pianka 1966). Animals may maximize energy intake per unit time feeding (Cowles *et al.* 1988; Belovsky 1997; Felton *et al.* 2009a). This hypothesis is usually tested in herbivores, mainly grazers (Belovsky 1984, 1997). Although it is rarely tested in primates due to the complexity of their diets (Milton 1979), some primate species may also maximise energy by allowing other nutrients to vary while keeping energy intake at a constant level (Strier 1992).

Dietary fibre generally refers to plant cell walls made up of cellulose, hemicellulose and pectin (Milton 1999). Most animals do not produce enzymes to breakdown cell walls to produce beneficial fatty acids and microbial proteins (Milton 1999; Felton *et al.* 2009a), which is why most primate species tend to minimize food items with high level of fibre contents in their diets (Davies *et al.* 1988; Barton & Whiten 1994; Yiming 2006; Hanya & Bernard 2015). An exception to this are the Colobines, who have a variety of anatomical specialisations to break down fibres into high quality fatty acids that can be used for energy (Dasilva 1992; Wasserman & Chapman 2003).

Plants have evolved secondary compounds to defend against a wide range of herbivores (Biere *et al.* 2004; Rosenthal & Berenbaum 2012). As a consequence, most

herbivores, including primates, tend to avoid food items with high concentrations of these compounds (Mckey *et al.* 1981; Glander 1982; Barton & Whiten 1994). This is due to the fact that most of secondary compounds are bitter-tasting and even toxic when consumed by animals (Acamovic & Brooker 2005). Although flowers (nectar and pollen), fruit, young leaves and mature leaves sometimes contain low to moderate concentrations of secondary metabolites including alkaloids, glycosides, tannins, and phenolics, some primate species have been observed feeding on these food items (Glander 1982; Barton & Whiten 1994). Some primates include secondary compounds such as particular tannins and alkaloids in their diet, which may be a form of self-medication, although this idea needs further investigation (Barton & Whiten 1994; Carrai *et al.* 2003).

Balancing nutritional intake is crucial to animal survival (Raubenheimer & Simpson 1997). As a result, animals (including primates) need to consume a variety of food sources to keep this balance (Whiten *et al.* 1991; Behie & Pavelka 2012b). Fruit and young leaves provide highly concentrated sources of simple sugar and protein, respectively (Felton *et al.* 2009c; Rothman *et al.* 2011; Hanya & Bernard 2015), but some primate species may also need to consume seeds to balance lipid concentrations (Whiten *et al.* 1991; Hanya & Bernard 2015). This need to balance nutrients often results in animals switching between food sources at different times of year to meet their nutritional targets, to ensure continued survival and reproduction (Felton *et al.* 2009c; Rothman *et al.* 2011; Behie & Pavelka 2012a).

1.7 Gibbons

Gibbons (Family: Hylobatidae) are the smallest apes, and are distributed in tropical forests in Asia (Mootnick & Fan 2011; Carbone *et al.* 2014; Veeramah *et al.* 2015). Their habitats are evergreen and semi-evergreen forests (Gray *et al.* 2010; Fan *et al.* 2011). They belong to the superfamily Hominoidea along with humans and the great apes (Carbone *et al.* 2014). There are 17 species of gibbons from four genera: *Symphalangus*, *Hylobates*, *Hoolock*, and *Nomascus* (Chatterjee 2009; Carbone *et al.* 2014; Veeramah *et al.* 2015), and are distributed across south China to Southeast Asia (Figure 1.4).



Figure 1.4: The geographical distributions of gibbons in south China to Southeast Asia. Cambodia has three species of gibbons from the genera *Nomascus* and *Hylobates*.
Source: Modified from Carbone *et al.* (2014).

Gibbon populations have declined significantly over the past three to four decades (Cheyne *et al.* 2008) and most species are listed as Critically Endangered or Endangered by the IUCN Red List (Gray *et al.* 2010) and CITES Appendix I (Geissmann 2007) due to the threats discussed above (Geissmann 2007; Cheyne *et al.* 2008; Phoonjampa & Brockelman 2008; Peng-Fei *et al.* 2009; Gray *et al.* 2010; Malone *et al.* 2014). For example, the total population of western hoolock gibbons (*Hoolock hoolock*) in India has declined by approximately 90% due to human disturbance, including habitat destruction, land use changes, and hunting (Kumar *et al.* 2009). The majority of threats to the yellow-checked crested gibbon (*N. gabriellae*) and pileated gibbon (*H. pileatus*) in Cambodia are habitat fragmentation, while hunting for meat and the pet trade are a secondary concern (Nadler *et al.* 2010; Rawson 2010b). Gibbons use trees not only for food sources, but also for calling (Nelson 2014), travelling and sleeping (Fan & Jiang 2008). Logging inside gibbons' habitat disturbs all of these behaviours (Peng-Fei *et al.* 2009). Sleeping trees selected by gibbons are generally tall, thick trees (Fan & Jiang 2008), and these are normally the target of loggers (Nelson 2014). This suggests that knowledge of tree and habitats selection by gibbons is urgently needed in order to allow governments or conservation agencies to protect these resources (Fan *et al.* 2011; Nelson 2014).

Fruit makes up the vast majority of gibbon diets, followed by young leaves, flowers, and seeds (McConkey *et al.* 2002; Fan *et al.* 2009; Fan *et al.* 2013), and occasionally insects (McConkey *et al.* 2002; Fan *et al.* 2013; Borah *et al.* 2014). Gibbons mainly select fruit that is yellow-orange in colour with small seeds and soft, juicy pulp (McConkey *et al.* 2002), but during times when fruit is scarce or unavailable, gibbons tend to shift their diet to leaves and flowers (Fan *et al.* 2013). The western black crested gibbons (*Nomascus concolor*) in Southern Yunnan have diets that consist of more than 70% fruit, while leaves only make up less than 20% of their diet (Fan *et al.* 2009). Similarly, most *Hylobates* consumes more fruit than leaves, flowers and insects (McConkey *et al.* 2002). Gibbons also spend time searching for insects (mainly cicadas, lepidopterans, and miscellaneous larvae) and the occasional bird chick as an alternative source of protein (Fan *et al.* 2013; Borah *et al.* 2014).

1.7.1 The genera *Symphalangus*, *Hylobates*, and *Hoolock*

The genus *Symphalangus* has only one species, siamang (*Symphalangus syndactylus*). However, due to the similarity between the morphology of *S. syndactylus* and *H. klossii*, particularly their shared black colouration, both species were initially thought to be the same genus (Geissmann 2002). The genus *Symphalangus* is distributed in peninsular Malaysia and Sumatra, Indonesia (O'Brien *et al.* 2004). *S. syndactylus* has the largest body weight (10-12 kg) compared to other gibbons, with both males and females reaching a similar size (Gittins & Raemaekers 1980). Moreover, the siamang produces a loud group call, and has a smaller home range than other gibbons (Chivers & MacKinnon 1977). Most female gibbons take care of an infant and are frugivorous, while male siamangs take responsibility for carrying offspring (Lappan 2008) and are folivorous (Elder 2009).

The genus *Hylobates* consists of seven species including the agile gibbon (*H. agilis*), kloss's gibbon (*H. klossii*), white-handed gibbon (*H. lar*), Javan gibbon (*H. moloch*), Bornean gibbon (*H. muelleri*), white-bearded gibbon (*H. albibarbis*) and the pileated gibbon (*H. pileatus*) (Strier 2007; Chatterjee 2009). This genus is distributed across south China to Cambodia, Thailand, Malaysia, and Indonesia (Ma *et al.* 1988; Geissmann 2007). The *Hylobates* are similar to other gibbons being frugivorous and monogamous (Chatterjee 2009; Elder 2009).

The genus *Hoolock* consists of two species, the western hoolock gibbon (*H. hoolock*) and the eastern hoolock gibbon (*H. leuconedys*) (Strier 2007). This genus is distributed in India, Myanmar and Yunnan province in China (Chetry *et al.* 2008), and is monogamous and frugivorous (Zhang *et al.* 2008). When young both males and females are black, but upon reaching maturity at age of five or six, females turn yellowish grey in colour (Islam & Feeroz 1992).

1.7.2 The genus *Nomascus*

The genus *Nomascus* was initially thought to only contain one species, *N. concolor* (Monda *et al.* 2007). However, seven species have since been identified: the western black crested gibbon (*N. concolor*), eastern black crested gibbon (*N. nasutus*), yellow-cheeked crested gibbon (*N. gabriellae*), white-cheeked crested gibbons (*N. siki*), hainan gibbon (*N. hainanus*), northern white-cheeked crested gibbons (*N. leucogenys*), and northern yellow-cheeked crested gibbons (*N. annamensis*) (Geissmann 2002; Thinh *et al.* 2010;

Mootnick & Fan 2011). There are four sub species of *N. concolor*: *N. c. concolor*, *N. c. lu*, *N. c. fuvogaster*, and *N. c. jingdongensis* (Mootnick & Fan 2011). The crested gibbons (*Nomascus. spp*) have shorter and denser hair than other gibbons, and are distributed across Cambodia, South China, Laos and Vietnam (Figure 1.5) (Mootnick & Fan 2011). The crested gibbons calls are slightly different from other species, in that mated pairs sing together, while non-mated individuals produce solo songs (Konrad & Geissmann 2006). They typically live in small family groups consisting of an adult male, an adult female, and any offspring (Fan *et al.* 2010). All crested gibbons are listed as Endangered or Critically Endangered by IUCN Red List (Gray *et al.* 2010; IUCN 2015), except *N. annamensis*, which has not yet been assessed, but it is thought to be Endangered (Vinh *et al.* 2010).

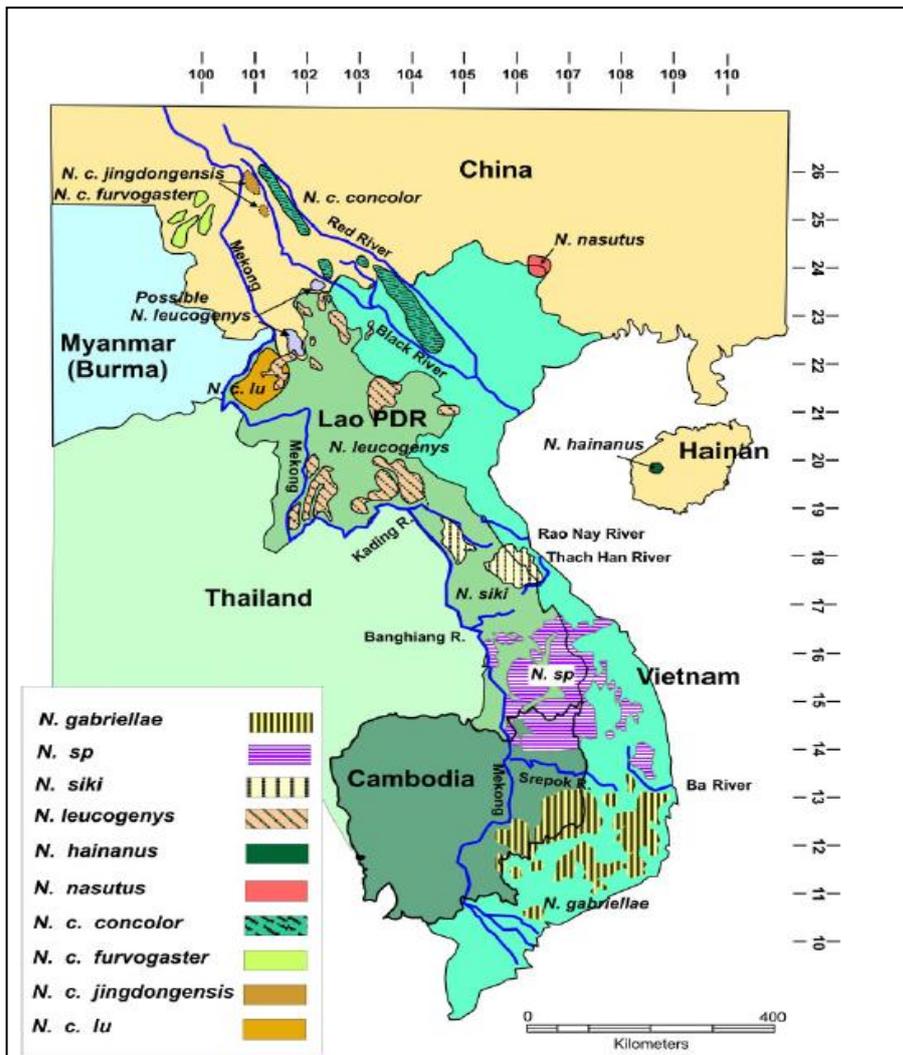


Figure 1.5: Distribution of *Nomascus. spp* in South China and Indochina regions. This map was created by M. Swartz and N. Ambar from IUCN Red List range maps, and surveys conducted by Pan P-F in South China. **Source:** Mootnick & Pan (2011).

1.7.2.1 The northern yellow-cheeked crested gibbon (*Nomascus annamensis*)

The northern yellow-cheeked crested gibbon is a newly-recognized species (Thinh *et al.* 2010). This species was thought to be *N. gabriellae* due the similarity of physical appearance; males of both species are black in colour with a yellowish-gold cheek patch and females are fully yellow in colour (Thinh *et al.* 2010; Vinh *et al.* 2010). However, northern yellow-cheeked crested gibbon is now recognised as a separate species distributed in northern Cambodia, Laos and Vietnam (Thinh *et al.* 2010), and most populations are declining due to habitat destruction and hunting (Long *et al.* 2011). Of these three countries, the largest population occurs in Cambodia (Rawson 2010a). They inhabit evergreen and semi-evergreen forests (Vinh *et al.* 2010), and plays a crucial role in seed dispersal (Frechette 2014).

Fruit is the main diet for *N. annamensis*, followed by young leaves, flowers and occasionally mature leaves and insects (Frechette *et al.* in prep). This species spends a considerable period of time resting, and the peak time for travelling and feeding occurs between 7 am and 10 am, and entering sleeping trees generally occurs around 4pm, in the late afternoon (Frechette *et al.* in prep). Gibbons, including crested gibbons, differ from other apes in that they do not build nests, but they use trees as their sleeping sites (Fan & Jiang 2008). A recent survey on sleeping tree selection by *N. annamensis* reveals that individuals select 11 species of trees to sleep in, with the most used species being *Dipterocarpus costatus*, *Shorea thorelii*, and *Anisoptera costata* (Nelson 2014). Of these, the family Dipterocarpaceae has economic value and is targeted for both timbers and resin by humans (Kao & Iida 2006), which puts this gibbon species in conflict with humans for this resource. These illustrating points of conflict and risk between humans and gibbons, is important for conservation measures, and will indicate those species that need protecting.

As with other endangered gibbon species, data about resource use and food selection are needed in order to create a successful long-term conservation plan for *N. annamensis*. Although it is known that *N. annamensis* selects predominately fruit, followed by young leaves and flowers, for their food sources (Frechette *et al.* in prep), knowledge is lacking on why they choose those specific plant species, what the main food plant species for this gibbon are, and what nutritional values these food sources have. The lack of this information creates difficulties for conservation planning. By increasing our understanding of food selection in *N. annamensis*, we will know which plant species are key resources and which main nutritional compositions are needed by this species. These

results will inform conservationists of those plant species that provide high quality food sources for *N. annamensis* in the wild, and the optimum nutritional composition of food that should be given to animals in captivity. Moreover, as the habitats of this species have been destroyed, these data will help the regeneration of habitats by growing specific key resources for this gibbon species. This will save time, money, and have a long-term positive effect on primate conservation. Providing this type of data for conservation efforts has helped the white-handed gibbon (*H. lar*), which became locally extinct in Phuket Island, Thailand in the 1980s (Osterberg *et al.* 2014). Eight families (30 individuals) of this species were reintroduced to the island in 2002 (Osterberg *et al.* 2015). When reintroducing a species to a habitat, knowledge of food availability and resource use by that species is key to supporting the new population (Tutin *et al.* 2001; IUCN/SSC 2013). In the case of the *H. lar* reintroduction, 10 years after the reintroduction just over half (16 individuals, 53%) of the original recolonizing population have survived on the island (Osterberg *et al.* 2015). Although many factors influence the failure and success of reintroduced populations, the availability of food sources could be one of the main factors (Taylor *et al.* 2005; Detedcc & Courchamp 2007). Therefore to best inform conservation of *N. annamensis*, data on food selection and resource availability are greatly needed.

1.8 Thesis overview

This is the first study on food selection by gibbons in Cambodia and to my knowledge is also one of the first on gibbons in general. This study was conducted at Veun Sai-Siem Pang Conservation Area (VSSPCA), northern Cambodia. This area has high biodiversity, with 60 species of mammals, 130 birds, and 60 reptiles (CI unpublished data). At least six species of primates were found in this area including red-shanked douc langurs (*Pygathrix nemaeus*), silvered langurs (*Trachypithecus germaini*) (Rawson & Bach 2011), long-tailed macaque (*Macaca fascicularis*), pig-tailed macaque (*Macaca leonina*), pygmy slow lorises (*Nycticebus pygmaeus*) (Hill 2011), and the study species, northern yellow-cheeked crested gibbon (*N. annamensis*) (Thin *et al.* 2010). As a result of these findings, the status of this area should be updated to “protected forest” in the near future. However, the area is currently under threat due to the impact of logging, hunting and pressure of over-use of natural resources inside the VSSPCA (pers. observation). By focusing on food selection in *N. annamensis*, we will gain a better understanding of the main diet of this species and what the key food resources and preferences are. As the

species is also threatened by illegal logging and habitat destruction, this information will increase and improve conservation by identifying important food resources that need to be protected. These data will also benefit captive rehabilitation and breeding programs and wildlife rescue centres, and help determine food types that have similar nutritional value to wild food sources for this species.

This thesis is organized into four chapters. As the two data chapters are formatted for publication, there is some repetition of material.

Chapter 1: General introduction

Chapter 2: Feeding behaviour and food plant selection

This chapter will address three basic questions. (1) Are there any differences in activity budgets among gibbons in the same group? (2) What are the main diets and key food species for the study group, and are there any differences in the group? (3) Does food availability influence food selection by this group?

Chapter 3: Nutritional values of food selected by *N. annamensis*.

This chapter focuses on the nutritional values of selected plant tissues and how nutritional values influence food selection. This chapter aims to answer two basic questions. (1) What are nutritional compositions of food items consumed by *N. annamensis*? This will focus on key food items consumed by *N. annamensis*, and the respective proportions of proteins, lipids, fibres, and some condensed tannins in each food item. Knowing the nutritional profile of food items can help identify why some species are eaten and others are not, and will identify important food species. (2) Using the “right-angled mixture triangle model” (Raubenheimer *et al.* 2015), what food items and nutritional compositions are targeted by *N. annamensis*? Answers to these questions will reveal for the first time the nutritional values of food items consumed by this group of *N. annamensis*. This chapter will also identify those plant species that should be protected, and which nutritional compositions should be given to the gibbons in captivity.

Chapter 4: General discussion. This chapter brings together the results of Chapters 2 and 3, discusses the results of food selection by *N. annamensis* with regard to other studies on food selection by primates, compares these findings with other relevant studies, and provides suggestions and recommendations for future research.

Chapter 2

Behavioural ecology and food plant selection

2.1. Introduction

Tropical regions exist extremely high plant diversity, with a large number of plant species in turn supporting a high density and diversity of other species (Gentry 1988; Clinebell II *et al.* 1995; Novotny *et al.* 2006). This is due to the diversity of food resources that these plant species provide all year round, including fruits, seeds, leaves, and flowers (Terborgh 1986). Between them, tropical plant species provide a diverse range of potential food sources, but not all plant species are selected by animals, with herbivores often selecting only specific plant species as food sources (Westoby 1974; Oates *et al.* 1980). This food selection by herbivores is guided in part by plant defence mechanisms (Palo & Robbins 1991). Some plant species have evolved both chemical and physical defences, which can render some plant species unsuitable for consumption by some herbivores (Wittstock *et al.* 2004; Rosenthal & Berenbaum 2012). To avoid foraging activity by herbivores, some plant species have evolved leaves with low nutritional quality and/or an increased range of unpalatable secondary compounds (Ryan 1989; Speiser & Rowell-Rahier 1991; Coley & Barone 1996), while others have developed thorns and trichomes to defend against numerous herbivores (Feeny 1976). Consequently, herbivores need to adapt to those defences, and select particular species for their food sources; some species even develop mutualisms with their hosts (Westoby 1974; Price *et al.* 1980; Wittstock *et al.* 2004).

The diets of the majority of primates include fruit, young leaves, flowers, seeds, and mature leaves (Cowles *et al.* 1988; Laska *et al.* 2000; Behie & Pavelka 2012a; Smith *et al.* 2013). However, primate diets differ dramatically among species (Davies *et al.* 1988; Strier 2007; Smith *et al.* 2013) depending on digestive physiology, habitat quality, nutritional needs and food availability. For example, both the Hylobatidae (gibbons) and Hominidae families (including orang-utans, chimpanzees, and gorillas) prefer fruit (Goodall 1986; McConkey *et al.* 2002; Boesch *et al.* 2006; Fan *et al.* 2009), whereas the specialised anatomy of the Colobinae allow them to ingest mainly young leaves (Hanya & Bernard 2012; Smith *et al.* 2013), and due to environmental pressure, some species even select mature leaves over other plant tissues (Behie & Pavelka 2012a). Generally, primates

are highly selective feeders, choosing not only specific plant tissues, but also specific plant species as their food sources (Davies *et al.* 1988; Fan *et al.* 2013; Smith *et al.* 2013). For example, a population of red leaf monkey (*Presbytis rubicunda*) in Malaysia predominantly feeds on rarer species, and the five dominant tree species in its home range, which make up over 80% of the total forest composition, comprise less than 7% of its diet (Davies *et al.* 1988). These illustrate that reasons for food selection in primates vary both among and within species, with some selecting food sources based on the availability of plant species, while others deliberately seek out comparatively rare plant species (Davies *et al.* 1988; Serio-Silva *et al.* 2002; Smith *et al.* 2013).

The northern yellow-cheeked crested gibbon (*Nomascus annamensis*) is a recently discovered species (Thinh *et al.* 2010) that is distributed across Cambodia, Laos, and Vietnam (Thinh *et al.* 2010; Long *et al.* 2011). There is a lack of data about this species, and furthermore, populations of *N. annamensis* have declined significantly due to habitat destruction and hunting (Rawson 2010b; Long *et al.* 2011). *N. annamensis* similar to other gibbons in that fruit forms the majority of its diet, followed by young leaves, flowers, mature leaves, and insects (Frechette *et al.* in prep). Although Frechette *et al.* (in prep) report on diet composition of this gibbon species, plant species selected are not identified and the relationship between food selection and food availability is also not mentioned.

An understanding of food resource use by threatened species like *N. annamensis* needed in order to create a long-term conservation plan. For example, knowledge of feeding tree selection contributed to the success of re-introductions of white-handed gibbons (*Hylobates lar*) into their natural habitats in Thailand (Osterberg *et al.* 2014). Frugivores like *N. annamensis* are especially under threat. It is due to the fact that the seasonal fluctuation of fruit production (Te Wong *et al.* 2005) and the removal of feeding trees inside gibbon territories can affect their populations (Johns 1986; Nijman 2001; Buckley *et al.* 2006). Scarcity of food could then in turn affect reproduction success and lifespan, having implications for population health (Thompson & Wrangham 2008; Mattison *et al.* 2012). This study focuses on food plant selection by *N. annamensis*, as well as addressing whether food availability influences food selection. With these objectives, three research questions have arisen. (1) Are there any differences in the activity budgets of gibbons in the same group? (2) What are the main plant parts and key food species selected by this gibbon group, and are there any differences among group members? (3)

Does food availability influence food selection by group members? The answers to these questions will show how many plant species are selected by this gibbon species, and whether they prefer rare or common plant species in their territory. This information can then be used to inform governmental agencies which plant species that need protection to assist the conservation of *N. annamensis*, not only in Cambodia, but also in all areas inhabited by this endangered gibbon. This information also can be used for gibbon rehabilitation programs, especially in areas where captive breeding of *N. annamensis* may be re-introduced.

2.2 Methods

2.2.1 Study site

The study was conducted at Veun Sai-Siem Pang Conservation Area (VSSPCA; 14° 01' N, 106° 44' E), a 55,000-ha site with an elevation between 100 - 400 m in Ratanakiri and Stung Treng provinces in northern Cambodia. This area is composed of evergreen and semi-evergreen forest, deciduous forest and grassland (Figure 2.1) (Geissler *et al.* 2012), and is located within the Indo-Burma biodiversity hotspot (Myers *et al.* 2000). The rainy season begins in May and lasts until October, while the dry season occurs from November to April. In the dry season, the mean minimum temperature is 15.5°C and the mean maximum temperature is 25.5°C, while in the rainy season the mean minimum temperature is 18°C and the mean maximum temperature is 23.5°C (Nelson 2014). The mean monthly rainfall in the rainy season is 189 mm (King *et al.* in review).

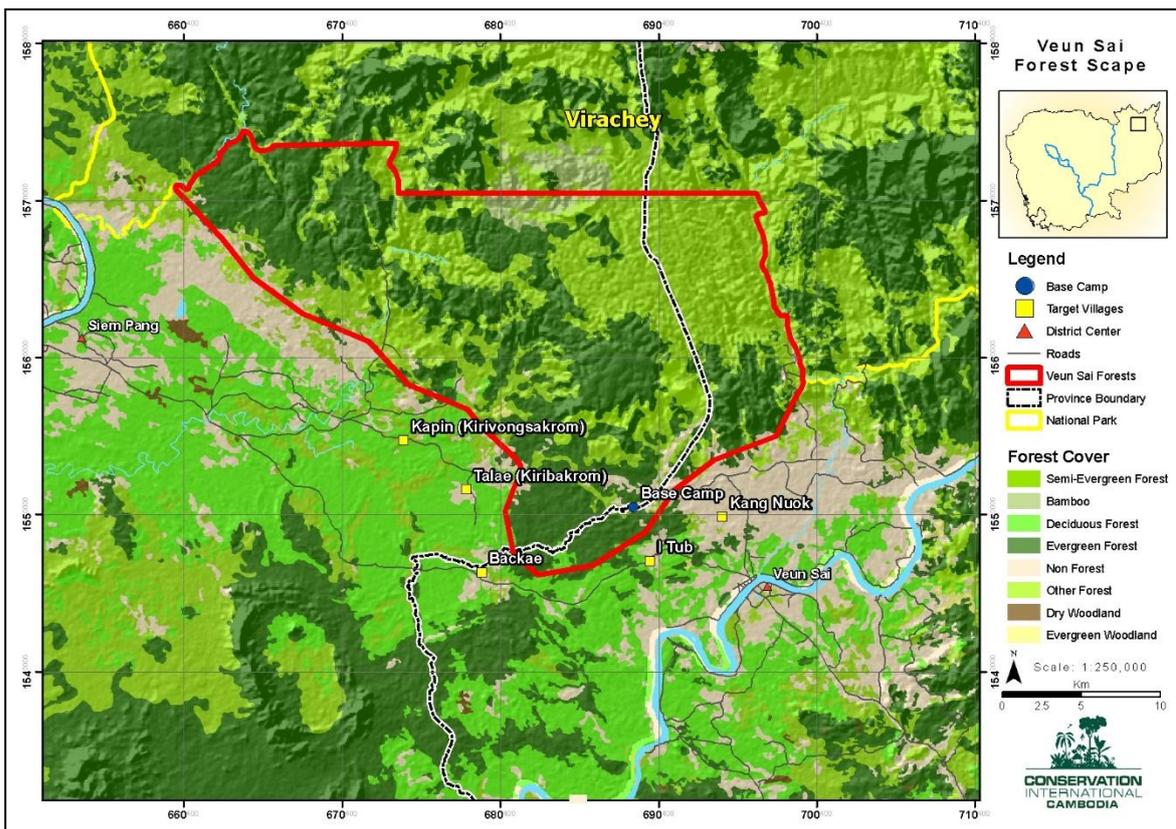


Figure 2.1: The Veun Sai-Siem Pang Conservation Area (VSSPCA), northern Cambodia (14° 01' N, 106° 44' E), outlined in red. Currently, this site is protected by the cooperation between Forestry Administration and Conservation International.

Image credit: Ben Rawson/Conservation International

2.2.2 Study Animals

A recent population survey of *N. annamensis* at VSSPCA revealed approximately 450 groups at the site (Rawson unpublished data). Due to a lack of data on this gibbon species, the first long-term study on its behaviour was established on one group of gibbons (called group A) in 2007 involving local, national and international researchers (Frechette *et al.* in prep). Currently, group A consists of five members: an adult male, an adult female, a sub-adult male, a juvenile male and an infant that was approximately 8 months old at the start of the study period (Figure 2.2). This group is now habituated to humans, which provides opportunities to observe them with minimum impact on their natural behaviours. The adults are easily distinguished, as the male is black and the female is yellow. Both the sub-adult male and juvenile male are black, but they can be distinguished by their body size. Group A is usually located about one hour walk from the main research station, and their territory is approximately 50 hectares in size.



Figure 2.2: Study group (Group A) of northern yellow-cheeked crested gibbons (*N. annamensis*) from Veun Sai-Siem Pang Conservation Area (VSSPCA), northern Cambodia. (a) the adult female, (b) the adult male, (c), the sub-adult male, and (d), the juvenile male, (e and f), the adult female and her baby. The colour of the adult female is changed according to the reflection of sun-light.

Photo: Naven Hon

2.2.3 Behavioural data collection

In total, 235 hours of focal animal data was collected over 40 days on group A. Four members of the group were observed for the study, and the infant was not included, as it was not weaned at the time of data collection. The study was conducted from mid-January until early April 2015. As gibbon groups are located by their morning vocalisations, behavioural observations began at 5:30 – 7:10 (calling time) until 11:00 or ~16:00. Each individual gibbon was observed for two different time periods, a half day from calling time to mid-day and a full day from calling time to early evening (sleeping time normally at 16:00). Each individual was observed equally for 5 half days and 5 full days ($N = 10$).

For each observation, the behaviours of the gibbons were recorded for 45 min per hour with a 15 min break before the next observation started. During observation, any change in behaviour was recorded. This allowed the exact time spent on each particular activity to be calculated. Activities recorded were resting, feeding, travelling, socializing, and 'out of observation'. Feeding was recorded when an individual gibbon was seen directly picking, chewing, swallowing and handling any food item (Fan *et al.* 2009). Resting was recorded in any situation where the focal gibbon did not move or was inactive. Travelling was recorded whenever the focal gibbon was moving. Socializing was noted when the focal animal saw playing, grooming and calling (for more detail, see Appendix 1). 'Out of observation' was noted when the focal animal could not be seen directly.

When the focal animal was feeding, the types of food item (species, and part of plant eaten) were recorded. The locations of those trees and lianas were marked with a handheld Global Position System (GPS) device (Garmin GPSMAP 62S) and the trees and lianas were labelled with species name and GPS waypoint. Photographs were taken of those species that could not be identified, for later identification by local people and to compare with a guide book (Phon 2000). If those plant species still could not be identified, they were named as unknown species. If the plant species still could not be identified, they were named as unknown species. Any illegal logging activities and human disturbance were noted during the observation period.

2.2.4 Ecological data

2.2.4.1 Phenological data

Phenological data were recorded in January, February and March 2015. Three transect lines within the home range of the gibbon study group were created by researchers from Conservation International (CI) and Forestry Administration (FA), and were used to collect phenological data in this study. These data included the percentage coverage (0%, 25%, 50%, 75%, and 100%) of plant tissues (fruit, flowers, young, and mature leaves). The percentage coverage of each tree and liana was assumed to be 100% including all those plant tissues. The percentage cover of each plant tissue was estimated by direct observation. For example, one tree could include 25% fruit, 25% flowers, 25% young leaves and 25% mature leaves, and another tree could be 100% mature leaves. For the purposes of this analysis, the contribution of branches and trunks to the total plant mass was ignored, as these tissues were not consumed by *N. annamensis*. Herbs and small shrubs were also not included in this analysis. Leaves were classified as young leaves from bud emergence until they reached full size and were lighter in colour (Behie & Pavelka 2012a), while mature leaves were fully expanded and darker in colour (Coley 1983). Ripe fruit and unripe fruit were identified based on their colours and physical examinations to determine if they were ripe or unripe.

2.2.4.2 Plant density

To estimate plant density and food availability, 20 vegetation plots (25 x 25 m) were randomly placed throughout the home range of group A during the study period (January-April 2015). Plant density was estimated from the 20 vegetation plots rather than from the transect lines because the trees and lianas on the transect line were biased towards feeding species, and therefore were not an accurate representation of the habitat. However, both plots and transect lines were located inside the home range of the gibbon study group. In each plot, all trees with a diameter at breast height (DBH) greater than 10 cm and liana species with a DBH greater 5 cm were measured and identified (Gerwing *et al.* 2006). These data were analysed to provide abundance, density, and dominance information on all tree and liana species throughout the home range of *N. annamensis*. Each tree and liana in each plot was tagged with a unique code number and recorded with GPS location. This

will be used for future research. Tree and liana species were identified by local researchers, with help from a guide book (Phon 2000). Local knowledge built up over seven years of studying this group of *N. annamensis* at this site allowed accurate identification of tree and liana species, particularly those used as food sources.

A food availability index (FAI) was calculated for the top 10 food species as recorded in this study. The gibbons fed on 37 different plant species (Table 2.3), but only the top 10 food plant species were selected for FAI analysis because only these 10 species overlapped inside the three transect lines and in the 20 vegetation plots. The FAI was determined for each plant tissue (fruit, flowers, and young leaves) for species *i* (Silver *et al* 1998), and defined (e.g. for fruit) as

$$FAI_{fr} = \sum_{1-i}(Di \times C_{fr,i}) \quad (1)$$

where FAI_{fr} is the FAI for fruit, Di is the density of tree or liana species *i*, and $C_{fr,i}$ is the average monthly coverage percentage for the fruit of that species. Similar FAIs were calculated for flowers (FAI_{fl}) and young leaves (FAI_{yl}). Gibbons did not feed on mature leaves from the top 10 plant species, so FAI_{ml} was not included in the analyses. However, the gibbons did consume mature leaves from other plant species. The density of species *i* was calculated as

$$Di = Ni / Nt \quad (2)$$

where Ni is the total number of stems of species *i*, and Nt is the total number of stems in the 20 vegetation plots.

2.2.5 Statistical analyses

The mean percentage time spent feeding, resting, travelling and socializing per day was calculated for each individual gibbon in the group. Similarly, the mean percentage of food type (fruit, flowers, young leaves, and mature leaves) each gibbon consumed per day was calculated. Both sets of data were non-normally distributed, thus non-parametric Kruskal-Wallis Tests were used to assess any differences between the time each individual spent on each activity, and any differences in food selection between individuals. Mann-

Whitney *U*-Tests were used to test the significance of the differences between each pair of activities (eg: resting and feeding) of individual gibbons, and to test the difference between time spent feeding in each pair food items (eg: fruit and young leaves). To assess the relationship between feeding time and food availability of fruit, young leaves, and flowers, Spearman's rank correlation tests were performed (Silver *et al.* 1998). All statistical analyses were performed in SPSS version 22, and in all cases $\alpha = 0.05$. A Bonferroni correction ($0.05/N$, i.e., $\alpha = 0.0125$) was used to adjust for multiple tests (Rice 1989).

2.3 Results

2.3.1 Activity budgets

The gibbons in group A generally spent similar amount of time on each activity together, and there was no statistically significant difference between the members of the group in their activity budgets (Kruskal-Wallis H test: all $P \geq 0.35$, Table 2.1. Figure 2.3). On average, the gibbons in group A spent most of their time resting (42.89%) and feeding (37.78%), with less time spent travelling (17.61%). The least amount of time was spent in social activities (1.72%) (Figure 2.3).

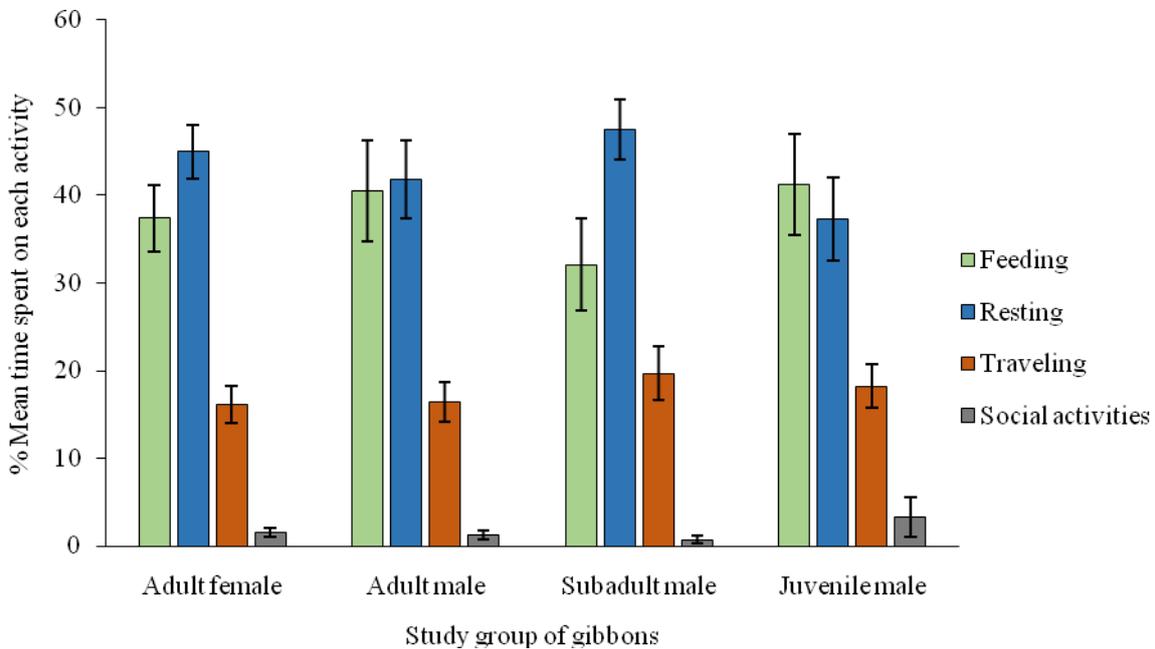


Figure 2.3: The average percentage of time that each individual gibbon spent on each activity, (feeding, resting, travelling and socializing) (\pm Standard error).

Table 2.1: Results of a Kruskal-Wallis H test comparing the mean percentage of time that individual gibbons spent feeding, resting, travelling and socializing.

Behaviours	$N(\text{days})$	$Chi\text{-square}$	$P\text{-value}$
Feeding	10	1.92	0.58
Resting	10	3.25	0.35
Travelling	10	0.67	0.87
Socializing	10	3.49	0.32

While all group members engaged in activities for similar proportions of time, there were significant differences in the amount of time the entire group engaged in different activities (feeding, resting, travelling and socializing) (all $P = 0.0001$, Table 2.2, Figure 2.3). Moreover, there were statistically significant differences between times that all individual gibbons spent time on most activities (Mann-Whitey U tests:all $P \leq 0.01$, Figure 2.3). However, the percentage of time that all individual gibbons spent feeding and resting were not significantly different (Mann-Whitey U tests:all $P \geq 0.07$, Figure 2.3). For more detail about each pairwise activity comparisons and significant values see Appendix 4, Table1.

The gibbons either hid, rested or moved out of observation when there was excessive noise (two cases of chainsaw and one case of tractor), especially when the noise of chainsaws from illegal loggings was close to the observation areas. Several cases of illegal loggings were observed around the VSSPCA (Appendix 2, Figure 1a and b). Moreover, although the gibbons in group A were habituated to humans, the gibbons avoided dogs and were suddenly out of observation when they saw domestic dogs with local researchers (one case).

Table 2.2: Results for Kruskal-Wallis H test comparing the mean percentage of time spent feeding, resting, travelling and socializing among *N. annamensis*.

Gibbons	<i>N</i>(days)	<i>Chi-square</i>	<i>P-value</i>
Adult female	10	32.41	0.0001
Adult male	10	30.11	0.0001
Sub-adult male	10	28.91	0.0001
Juvenile male	10	26.02	0.0001
Overall gibbons	40	120.20	0.0001

When comparing activity by month, the gibbons in group A spent a similar amount of time feeding (38.80%) and resting (44.49%) in January, more than travelling (14.34%) and socializing (2.37%). In contrast, the time spent feeding increased to 49.06% in February, while resting dropped to 37.06%. In March, the time spent feeding declined to 28%, whereas resting and travelling increased to 49.55% and 21.44% respectively. The gibbons spent the least amount of time in social activities in all three months (Figure 2.4).

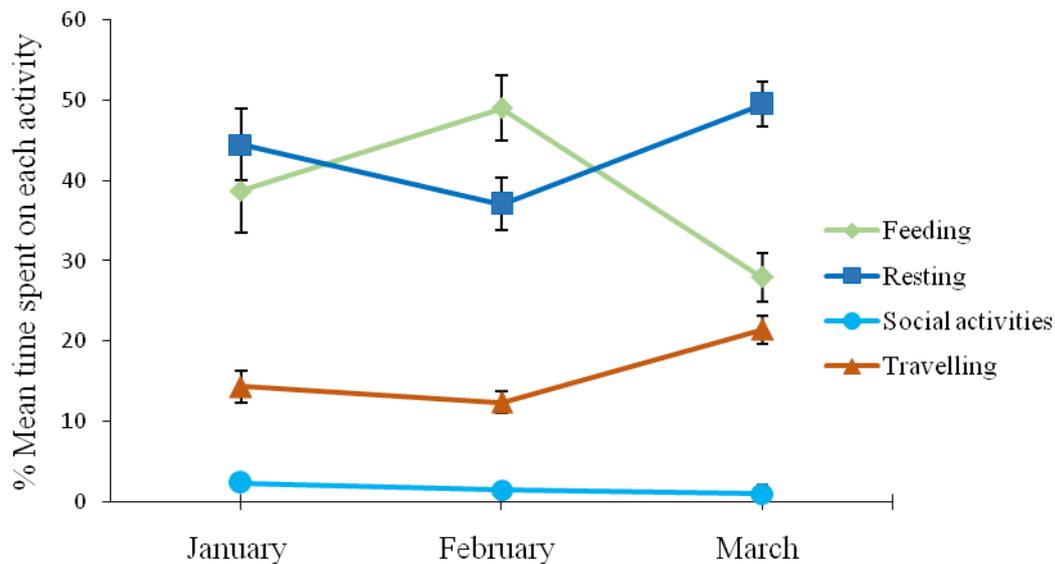


Figure 2.4: The average percentage of time that gibbons in group A spent on each activity budget from January to March 2015 (\pm standard error).

2.3.2 Food plant selection

In total, the gibbons fed on 37 different plant species from more than 17 families, and these plant species were distributed evenly inside their home range (Figure 2.5) of which 18 species were trees (48.65%), 17 species were lianas (45.94%) and two species were epiphytes (5.41%) (Table 2.3). Twenty-one species were fed on for less than 1% of the feeding time, however the top 16 species (feeding time more than 1% in the diet) made up 88.83% of the overall diet (Table 2.3). The gibbons were occasionally observed feeding on insects, spiders and larvae, although the species were not identified (Appendix 2, Figure 2). The gibbons were also observed feeding on honey bees and bee larvae.

Table 2.3: Plant species selected by group A of *N. annamensis*, including the time they spent feeding each species and the tissue consumed from January until early April 2015 in northern Cambodia. Percentage here represents the amount of time that the gibbons spent feeding all food plant species. The species are ranked according to the time spent feeding those species (highest to lowest) with the line draw under the top 16 species. Months here refer to the periods that the gibbons selected the food items.

Family	Species	Time (%)	Rank	Form	Plant tissue	Months
Aquifoliaceae	<i>Ilex umbellulata</i>	22.13	1	T	F/Fr	Feb/Mar
Moraceae	<i>Ficus. sp</i>	14.56	2	L	Fr	Jan/Feb/Mar
Fagaceae	<i>Lithocarpus elegans</i>	9.50	3	T	YL	Jan/Feb/Mar
Guttiferae	<i>Garcinia oliveri</i>	6.91	4	T	YL/F	Jan/Feb/Mar
Apocynaceae	<i>Willughbeia edulis</i>	6.62	5	L	Fr/YL	Feb/Mar/Apr
Dipterocarpaceae	<i>Dipterocarpus alatus</i>	5.89	6	T	F	Feb/Mar
Gnetaceae	<i>Gnetum macrostachyum</i>	3.68	7	L	Fr	Jan/Feb/Mar
Leguminosae	<i>Dialium cochinchinensis</i>	3.20	8	T	YL	Feb/Mar
Sapotaceae	<i>Madhuca elliptica</i>	3.12	9	T	Fr	Mar/Apr
Anacardiaceae	<i>Mangifera duperreana</i>	2.78	10	T	YL	Feb
Unknown	Unknown-1	2.16	11	T	YL	Jan/Feb
Unknown	Kbal Thum	2.01	12	T	Fr	Feb/Mar
Unknown Liana	Vor Krovanh (LN)	1.71	13	L	YL	Feb/Mar
Unknown	Unknown-2	1.69	14	T	YL	Jan
Unknown Liana	Chrey Slekthum (LN)	1.64	15	L	ML	Feb
Apocynaceae	<i>Dischidia. sp</i>	1.23	16	E	ML	Jan
Unknown Liana	Vor Antong (LN)	0.93	17	L	YL	Jan/Feb
Unknown Liana	Vor Tang Ant (LN)	0.79	18	L	YL	Jan/Feb
Unknown	Unknown-4	0.46	19	T	YL	Jan/Feb
Ochnaceae	<i>Ochna atropurpurea</i>	0.35	20	T	F/YL	Feb/Mar
Dipterocarpaceae	<i>Anisoptera costata</i>	0.34	21	T	YL	Jan
Unknown	Unknown-3	0.28	22	T	YL	Jan/Feb
Moraceae	<i>Ficus racemosa</i>	0.24	23	T	Fr	Mar
Meliaceae	<i>Aglaia grandis</i>	0.24	24	T	Fr	Jan
Unknown	Unknown-5	0.12	25	T	YL	Jan
Myrtaceae	<i>Syzygium. sp</i>	0.06	26	T	YL	Jan
Unknown	Other Unknown Species*	5.74	27-37	L	YL	Jan/Feb/Mar
Arthropods	Spiders/Insects/Larvae	0.56		A		Jan/Feb/Mar
Water	Drinking water	1.06		W		Mar

Key: A = animal, T= tree, L=liana, E= epiphyte, YL= young leaves, ML= mature leaves, F= flowers, Fr= fruit, and W= water, LN = local name. Other unknown species* = Unidentified food plant species (11 species).

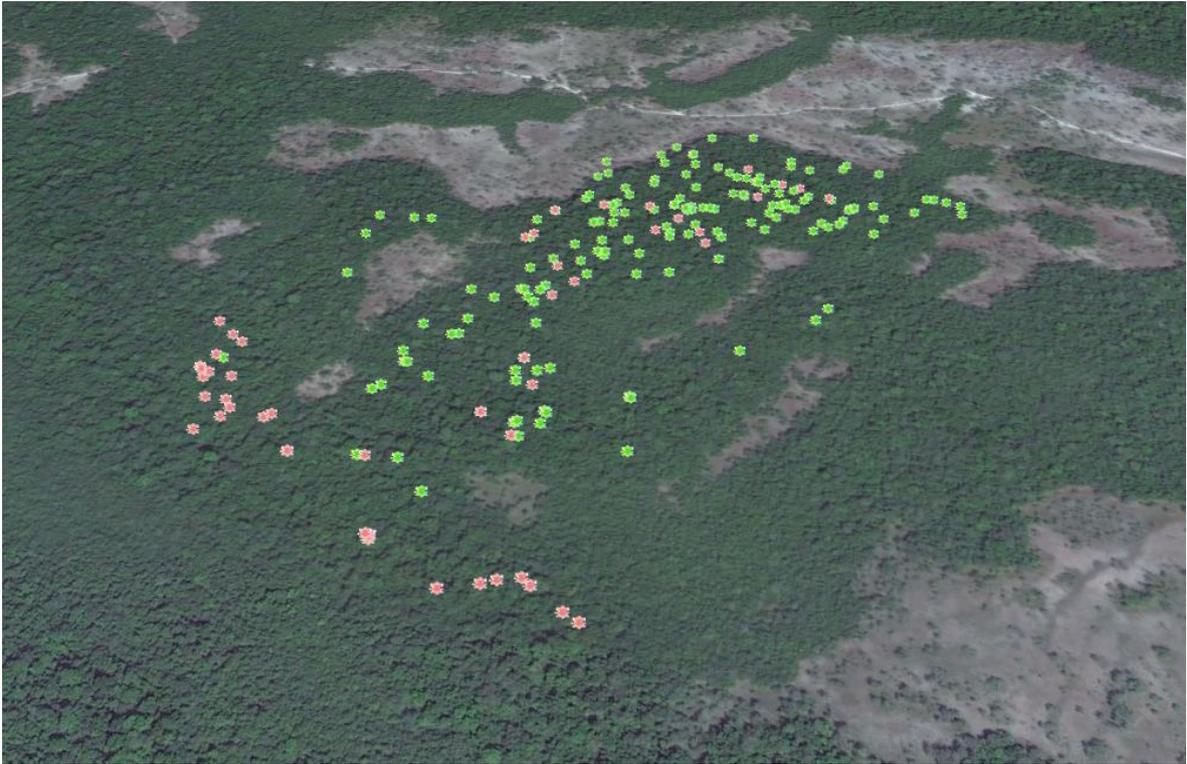


Figure 2.5: Distribution of food plant tree and liana species selected by the group of *Nomascus annamensis* at VSSPCA, northern Cambodia. The green stars refer to the top 10 feeding plant species, while the pink stars refer to the rest of feeding plant species. These data are based on the GPS locations of each species recorded during observation periods. The dark-green is evergreen and semi-evergreen forest, while grey-brown spots are deciduous forests.

Image credit: Google Earth, created by Kuthet Sok

2.3.3 Diet budgets

All group members of *N. annamensis* had similar diets with no statistically significant differences in time spent feeding on each food types among group members (Kruskal-Wallis H test: all $P \geq 0.53$, Table 2.4, Figure 2.6). When all 37 plant species consumed by gibbons in group A were considered, fruit was the most preferred food in each gibbon's diet, making up 60.36%, followed by young leaves (22.60%), flowers (13.74%), and mature leaves (3.30%). The gibbons mostly consumed only the flesh of the fruit, and generally spat out the seeds (Appendix 2, Figure 4), although some small fruits were swallowed with seeds. For example, the gibbons usually consumed only flesh from *W. edulis* and *M. elliptica*, while *I. umbellulata* and *G. macrostachyum* were swallowed with their seeds. Of the fruit selected, the gibbons mainly chose ripe fruit

(87%) over unripe (11%) and mature fruit (2%). The common unripe fruits consumed was: *I. umbellulata* (Appendix 2, Figure 5), while mature fruit was *A. grandis* (Appendix 2, Figure 6). The two adults were observed consuming mature leaves of an unknown liana species and one species of epiphyte (small leaves) (4.33 - 4.46%). The other two individuals (sub-adult and juvenile male) consumed mature leaves only very rarely (0.1-0.74%). One species of epiphyte was chewed and sucked, and then spat out, providing only liquid nutritional values (Appendix 2, Figure 7).

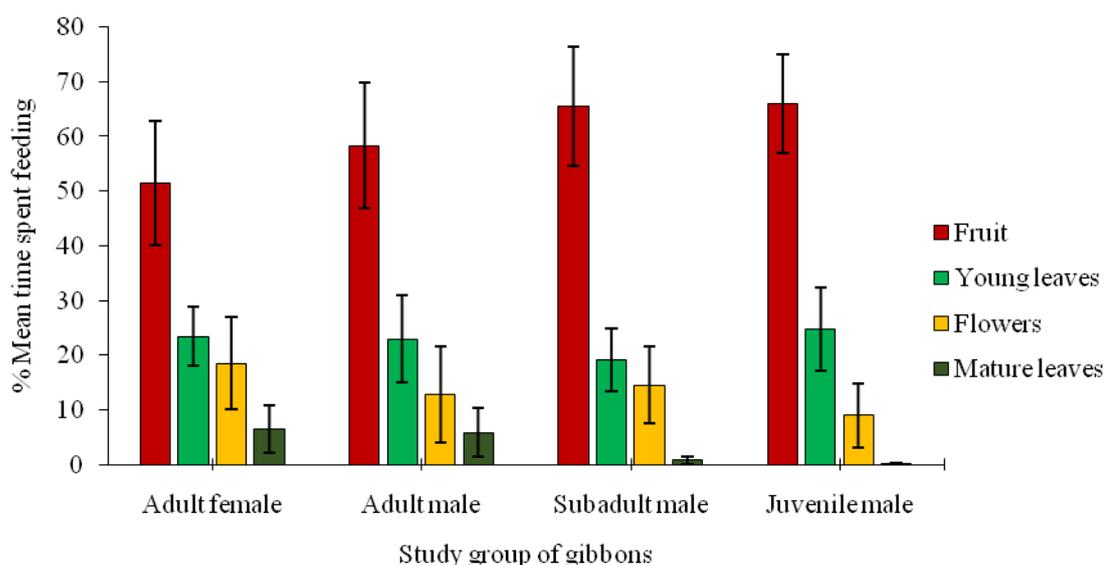


Figure 2.6: The average percentage of time that each gibbon spent consuming fruit, young leaves, flowers and mature leaves from all 37 sources of food items (\pm standard error).

Table 2.4: Results of a Kruskal-Wallis H test comparing the mean percentage time that each gibbon spent feeding different food types (fruit, young leaves, flowers, and mature leaves)

Plant tissues	N (days)	Chi -square	P -value
Fruit	10	1.37	0.71
Young leaves	10	0.63	0.88
Flowers	10	0.94	0.81
Mature leaves	10	2.20	0.53

Generally, the gibbons, both individually and as a group, spent significantly different amounts of time feeding on each plant tissue (fruit, young leaves, flowers, and mature leaves) (Kruskal-Wallis H test: individually: $P \leq 0.01$; group: $P = 0.0001$, Table 2.5,

Figure 2.6). All group members of gibbons spent significant more time feeding on fruit than young leaves, flowers, and mature leaves (Mann-Whitney U tests: all $P \leq 0.01$, Figure 2.6). Moreover, both the sub-adult male ($U = 16.5$, $P = 0.01$) and the juvenile male ($U = 11$, $P = 0.003$) spent significantly more time feeding on young leaves than mature leaves, while both the adult female ($U = 19.5$, $P = 0.02$) and the adult male ($U = 19$, $P = 0.02$) spent similar amount of time feeding on young leaves and mature leaves. No significant differences were found in feeding time for young leaves, flowers and mature leaves for all gibbons (Mann-Whitney U tests: all $P \geq 0.04$). For more detail of each pairwise comparison and significant values see Appendix 4, Table 2.

Table 2.5: Results of a Kruskal-Wallis H test comparing the mean percentage time spent feeding different food types (fruit, young leaves, flowers and mature leaves) by each individual gibbon in group A.

Gibbons	<i>N</i>(days)	<i>Chi-square</i>	<i>P-value</i>
Adult female	10	11.13	0.01
Adult male	10	13.82	0.003
Sub-adult male	10	19.60	0.0001
Juvenile male	10	26.23	0.0001
Overall gibbons	40	72.96	0.0001

The gibbons spent similar time feeding on young leaves (33.45%), flowers (28.40%), and fruit (27.51%) in January, while mature leaves were the least consumed food (10.64%). In contrast, the time spent feeding on fruit increased to 46.25% in February and 82.80% in March, while the time spent feeding on young leaves and flowers declined from 26.59% to 16.17% and 25.13% to 1.04%, respectively. The gibbons continued to spend less time feeding on mature leaves in February (2.03%) and did not feed on mature leaves at all in March (Figure 2.7).

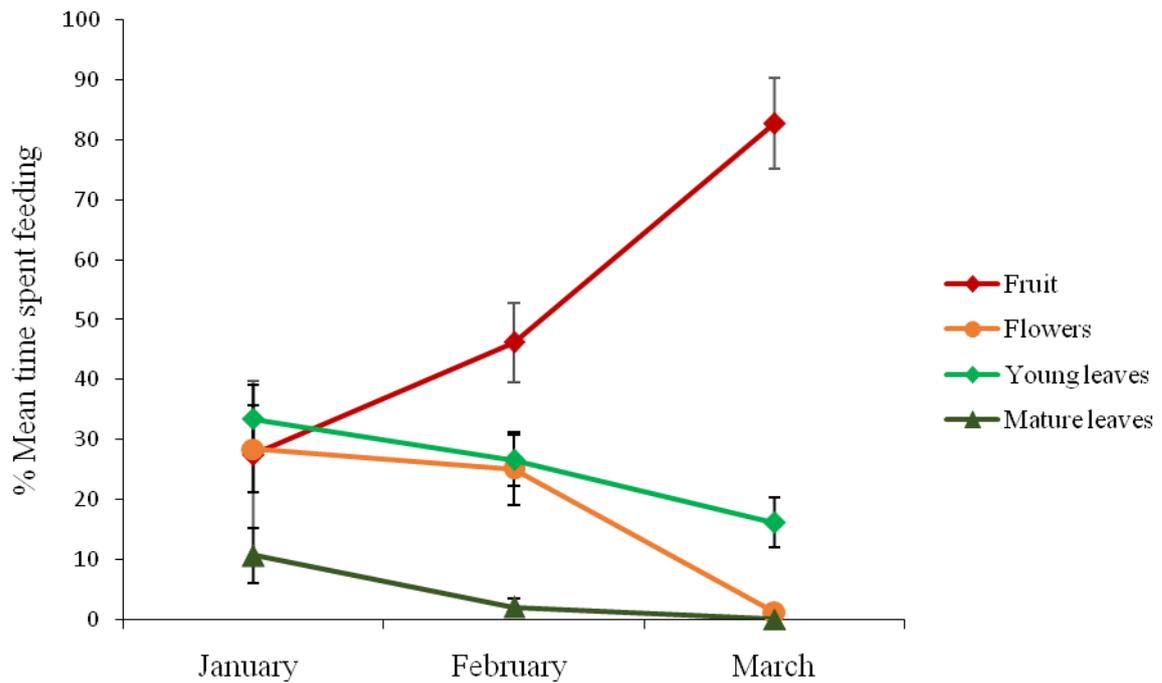


Figure 2.7: The average percentage time that the group of *Nomascus annamensis* spent consuming fruit, young leaves, flowers and mature leaves from January to March 2015 (\pm standard error).

2.3.4 Food availability

2.3.4.1 Phenology

The percentage coverage of plant tissues during the study period was determined from fixed transects set within the home range of gibbons in group A. The fruit coverage was very low in January (1.21%) and highest in March (4.23%). This is due to the fact that in January, only about 3% of plants bore fruit, whereas 8% were fruiting in February and 10% in March. Among the top 10 feeding species, *Ficus. sp* and *G. macrostachyum* bore fruit for the entire period of data collection (January - March), while *I. umbellulata*, *M. elliptica*, and *W. edulis* began bearing fruit in February. The coverage of flowers and young leaves were also low (0.66 - 2.91% and 11.53 - 13.11%, respectively), while the bulk of the plant material was mature leaves (82.17 - 83.21%) (Figure 2.8).

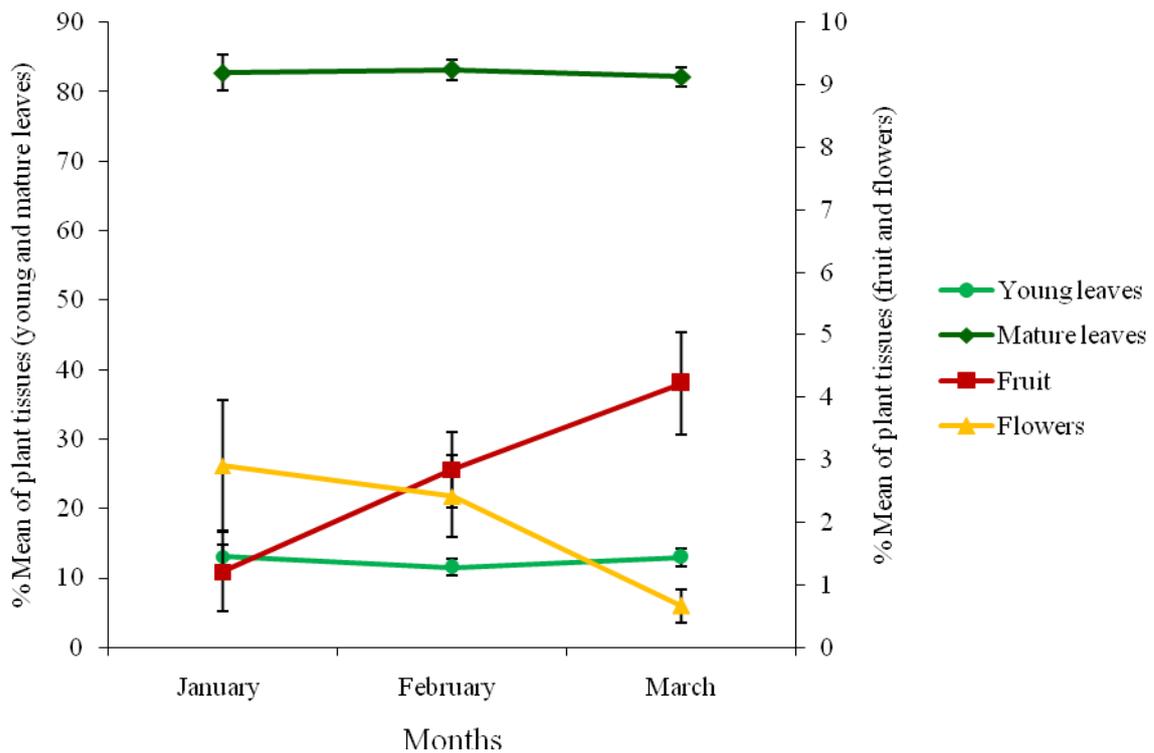


Figure 2.8: The coverage percentage of fruit, flowers, young leaves, and mature leaves between January and March 2015 in Veun Sai-Siem Pang Conservation Area (VSSPCA), northern Cambodia. Fruit and flower are represented on the right axis, while the left axis shows young and mature leaves. This data was obtained from fixed phenology transect lines within the home range of gibbons in group A (\pm standard error).

2.3.4.2 Vegetation plots

In total, 969 individual trees and lianas were recorded inside the 20 vegetation plots, comprising more than 74 different species (including some unidentified species), of which 80% were trees, and 20% were lianas. Of these, 16 were food species of the gibbons – with 11 being food trees and 5 being food lianas. This represents a total food plant density of 77% and a basal area of $34.55 \text{ m}^2 \cdot \text{plot}^{-1}$ for food species within the sampled area (trees $34.22 \text{ m}^2 \cdot \text{plot}^{-1}$ and lianas $0.34 \text{ m}^2 \cdot \text{plot}^{-1}$) (Table 2.6). The number of food plant species in the plots (16 species) differed from the food plants noted during observation (46 species) because some plant species were not found inside the sampled plots. Based on these plots, *Lithocarpus elegans* was the third most abundant species in the gibbon’s home range (Table 2.6), and this species was also the third highest source of food for group A (Table 2.6). *Nephelium mutabile* and Nang Kmov (local name) were even more abundant than *L. elegans* (Table 2.6), but these trees did not bear fruit or produce flowers during the

study periods. Thus, although these two dominant tree species are known to the local guides as common sources of food (particularly for fruit), the gibbons were not observed consuming any plant parts from them during the study periods. Similarly, other tree and liana species are sources of food according to local knowledge, but the gibbons did not consume any parts of these species during this study (Table 2.6, last column). Most plant species consumed by the gibbons were rare in the home range of this gibbon study group, with the two most commonly eaten species, *I. umbellulata* and *Ficus. sp* comprising only 0.82% and 0.41% of the total canopy in the plots, respectively (Table 2.6).

Table 2.6: The relative density and average basal area of trees and lianas as determined from the 20 vegetation plots inside the home range of gibbon group A. Species in bold are the top 10 species used for food by the study group of *N. annamensis* from January until early April 2015 in northern Cambodia, and the rank in their diet (Table 2.2) is given in brackets. Tree and liana species that were consumed during the study period are listed under the food column. Other tree and liana species that are known from local knowledge to be food species are also indicated.

Species/local name	Life form	Rank	Relative density	Average of basal area (m ²)	Food	Food (local knowledge)
<i>Nephelium mutabile</i>	T	1	0.180	55.55	No	Yes
Nang Kmov (LN)	T	2	0.144	35.83	No	Yes
<i>Lithocarpus elegans</i> (3)	T	3	0.137	67.57	Yes	Yes
<i>Syzygium. sp</i>	T	4	0.065	55.04	Yes	Yes
Unknown-sp	T	5	0.063	31.96	No	Yes
<i>Sterculia lychnophora</i>	T	6	0.033	8.99	No	Yes
<i>Aglaia odorata</i>	T	7	0.027	4.91	No	No
<i>Willughbeia edulis</i> (5)	L	8	0.025	1.98	Yes	Yes
Aihoun (LN)	T	9	0.017	4.21	No	No
Dom Sambok Krohom (LN)	T	10	0.016	4.25	No	Yes
<i>Madhuca elliptica</i> (9)	T	11	0.014	8.63	Yes	Yes
<i>Bouea oppositifolia</i>	T	12	0.013	8.88	No	Yes
<i>Gnetum macrostachyum</i> (7)	T	13	0.012	0.81	Yes	Yes
Kbal Thum (LN)	T	14	0.012	41.51	Yes	Yes
<i>Irvingia malayana</i>	T	15	0.010	69.55	No	Yes
Tang Ant (LN)	L	16	0.010	0.74	Yes	Yes
<i>Anisoptera costata</i>	T	17	0.009	13.14	No	Yes
<i>Cinnamomum cambodian</i>	T	18	0.009	1.80	No	Yes
Dom Atchor (LN)	T	19	0.009	2.73	No	No
<i>Shorea thorelii</i>	T	20	0.009	12.48	No	No
Tong Nam (LN)	T	21	0.009	2.07	No	Yes
<i>Ilex umbellulata</i> (1)	T	22	0.008	4.71	Yes	Yes
Klang Kan Trong (LN)	T	23	0.008	6.61	No	No
<i>Nephelium hypoleucm</i>	T	24	0.008	2.29	No	Yes
<i>Diospyros nitida</i>	T	25	0.007	1.48	No	No
<i>Albizia myriophylla</i>	T	26	0.006	2.93	No	No
<i>Albizia. sp</i>	T	27	0.006	4.01	No	No
Antong (LN)	L	28	0.006	0.25	Yes	Yes
<i>Dipterocarpus alatus</i> (6)	T	29	0.006	35.37	Yes	Yes

Species/local name	Life form	Rank	Relative density	Average of basal area (cm ²)	Food	Food (local knowledge)
Dom Mek Tech (LN)	T	30	0.006	2.31	No	Yes
Garcinia oliveri (4)	T	31	0.006	3.40	Yes	Yes
<i>Parinari annamensis</i>	T	32	0.006	4.47	No	Yes
<i>Ochna atropurpurea</i>	T	33	0.005	0.68	Yes	Yes
<i>Calophyllum calaba</i>	T	34	0.004	1.86	No	Yes
Ficus. sp (2)	L	35	0.004	2.20	Yes	Yes
Khov Keb (LN)	T	36	0.004	0.50	No	Yes
Mak Dekkouy (LN)	T	37	0.004	0.77	No	Yes
Mangifera duperreana (10)	T	38	0.004	3.06	Yes	Yes
Smach (LN)	T	39	0.004	0.89	No	Yes
Vor Sleng (LN)	L	40	0.004	0.69	No	Yes
Dialium cochinchinensis (8)	T	41	0.003	2.12	Yes	Yes
Dom Sleik Toch (LN)	T	42	0.003	0.55	No	No
Douk Kouy (LN)	T	43	0.003	1.16	No	Yes
Krovanh (LN)	L	44	0.003	0.14	Yes	Yes
Sidong (LN)	T	45	0.003	1.68	No	No
<i>Sindora cochinchinensis</i>	T	46	0.003	6.15	No	Yes
<i>Aglaia leptantha</i>	T	47	0.002	0.47	No	Yes
<i>Antidesma cochinchinensis</i>	T	48	0.002	0.31	No	Yes
Chhor tree (LN)	T	49	0.002	6.68	No	No
Dom man chor (LN)	T	50	0.002	0.21	No	No
Dom Sambok Kras (LN)	T	51	0.002	0.77	No	No
<i>Hopea. sp</i>	T	52	0.002	6.80	No	No
<i>Microcos paniculata</i>	T	53	0.002	1.46	No	Yes
Mok (LN)	T	54	0.002	13.24	No	No
Mout (LN)	T	55	0.002	0.46	No	No
Vor Sor (LN)	L	56	0.002	0.17	No	Yes
<i>Carallia brachiata</i>	T	57	0.001	1.06	No	Yes
Chan Kikai (LN)	T	58	0.001	0.12	No	No
Cheng Tea (LN)	T	59	0.001	2.28	No	No
Dom Koung (LN)	T	60	0.001	0.11	No	No
Dom Sambok Sdeang (LN)	T	61	0.001	0.18	No	No
Dom Sambok sor (LN)	T	62	0.001	0.31	No	No

Species/local name	Life form	Rank	Relative density	Average of basal area (cm ²)	Food	Food (local knowledge)
Dom Sambok Sroy (<i>LN</i>)	T	63	0.001	0.16	No	No
Dom SleK Kras (<i>LN</i>)	T	64	0.001	0.21	No	No
Ham Oav (<i>LN</i>)	T	65	0.001	3.75	No	No
Kam Pul Bay (<i>LN</i>)	T	66	0.001	0.26	No	No
Khai Phai (<i>LN</i>)	T	67	0.001	0.59	No	No
Ki Nu (<i>LN</i>)	T	68	0.001	0.15	No	No
<i>Nephelium. sp</i>	T	69	0.001	0.19	No	Yes
Plea Keave (<i>LN</i>)	T	70	0.001	0.12	No	Yes
Rang Phnom (<i>LN</i>)	T	71	0.001	0.12	No	Yes
Romdoul (<i>LN</i>)	T	72	0.001	0.14	No	Yes
Sayak (<i>LN</i>)	T	73	0.001	0.22	No	Yes
<i>Shorea cochinchinensis</i>	T	74	0.001	0.99	No	No

LN= local name, RD = relative density, T = tree, L= liana

2.3.4.3 Relationship between food availability and food consumption

The total FAI_{fr} from the top 10 species increased 10-fold from 0.21 in January to 2.29 in March (Table 2.7). Although FAI_{fr} increased, no statistically significant relationship was found between feeding time and FAI_{fr} ($r_s = 0.09$, $P = 0.76$, $N = 12$, Figure 2.9a). This may be due to the fact that the relative densities of fruit bearing trees that gibbons selected were very low inside their home range. However, those trees produced an abundance of fruit during the study period, and this led the group to increase feeding on fruit of those specific species. For example, the FAI_{fr} for *Ficus. sp* did not change over the three month period, but the amount of time feeding on this item did with the most time ingesting *Ficus. sp* fruit occurring in February. However, the relative density of *Ficus. sp* was only 0.004 (0.4% of the total plant density). The total of FAI_{yl} from the top 10 species increased slightly from 3.44 in January to 5.32 in February, but declined to 4.25 in March (Table 2.7). As a result, there was no statistically significant relationship between feeding time and FAI_{yl} ($r_s = 0.30$, $P = 0.36$, $N = 9$, Figure 2.9b). The total FAI_{fl} from the top 10 species increased from 0.39 in January to 0.72 in February. Although it declined to 0.38 in March (Table 2.7), there was a significant relationship between feeding time and FAI_{fl} ($r_s = 0.82$, $P = 0.04$, $N = 6$, Figure 2.9c). *D. alatus* and *G. oliveri* were important sources of flowers, especially in February when flowers became more available, and the gibbons spent more time feeding on these tree species (Table 2.7).

Table 2.7: Food availability index (FAI) for each of the top 10 species found in quadrats for January, February and March 2015. For FAI columns and rows, “0” values indicate those plants that did not bear fruit, flowers or leaves. Values in bold refer to those plant species that were eaten by gibbons. Values not bold show plants that produced edible tissues that gibbons were not observed feeding on them.

Species	Months	Timespent feeding (%) on all plant tissues	FAI(fr)	FAI(fl)	FAI(yl)	FI (ml)
<i>Ficus. sp</i>	Jan	24.25	0.14	0.00	0.03	0.24
<i>Garcinia oliveri</i>	Jan	16.83	0.00	0.22	0.09	0.25
<i>Gnetum macrostachyum</i>	Jan	1.10	0.08	0.00	0.00	1.16
<i>Ilex umbellulata</i>	Jan	0.77	0.00	0.17	0.14	0.51
<i>Willughbeia edulis</i>	Jan	0.58	0.00	0.00	0.31	2.16
<i>Lithocarpus elegans</i>	Jan	0.22	0.00	0.00	2.66	11.02
<i>Dialium cochinchinensis</i>	Jan	0.00	0.00	0.00	0.10	0.21
<i>Madhuca elliptica</i>	Jan	0.00	0.00	0.00	0.00	1.44
<i>Mangifera duperreana</i>	Jan	0.00	0.00	0.00	0.04	0.37
<i>Dipterocarpus alatus</i>	Jan	0.00	0.00	0.00	0.00	0.62
Total (eaten + not eaten)		43.75	0.21	0.39	3.44	17.98
<i>Ficus. sp</i>	Feb	19.55	0.14	0.00	0.10	0.17
<i>Lithocarpus elegans</i>	Feb	14.56	0.00	0.00	3.80	9.88
<i>Dipterocarpus alatus</i>	Feb	12.94	0.00	0.31	0.15	0.15
<i>Ilex umbellulata</i>	Feb	10.26	0.25	0.11	0.07	0.39
<i>Garcinia oliveri</i>	Feb	7.76	0.00	0.25	0.09	0.28
<i>Gnetum macrostachyum</i>	Feb	6.78	0.54	0.00	0.31	0.39
<i>Mangifera duperreana</i>	Feb	6.50	0.00	0.00	0.17	0.24
<i>Dialium cochinchinensis</i>	Feb	1.92	0.00	0.00	0.13	0.18
<i>Willughbeia edulis</i>	Feb	1.78	0.62	0.00	0.46	1.39
<i>Madhuca elliptica</i>	Feb	0.95	0.20	0.06	0.03	1.16
Total (eaten + not eaten)		83.00	1.74	0.72	5.32	14.23
<i>Ilex umbellulata</i>	Mar	46.37	0.34	0.00	0.03	0.45
<i>Willughbeia edulis</i>	Mar	18.43	0.93	0.00	0.00	1.54
<i>Madhuca elliptica</i>	Mar	9.78	0.42	0.03	0.15	0.84
<i>Lithocarpus elegans</i>	Mar	9.14	0.00	0.00	3.52	10.16
<i>Dialium cochinchinensis</i>	Mar	5.87	0.00	0.00	0.10	0.21
<i>Ficus. sp</i>	Mar	3.30	0.14	0.00	0.00	0.27
<i>Gnetum macrostachyum</i>	Mar	1.38	0.46	0.00	0.15	0.62
<i>Dipterocarpus alatus</i>	Mar	0.86	0.00	0.23	0.15	0.23
<i>Garcinia oliveri</i>	Mar	0.55	0.00	0.12	0.12	0.37
<i>Mangifera duperreana</i>	Mar	0.00	0.00	0.00	0.00	0.41
Total (eaten + not eaten)		95.68	2.29	0.38	4.24	15.10
Total (Jan + Feb + Mar)			4.24	1.49	13.00	47.31

FAI = food availability index, (fr) = fruit, (fl) = flowers, (yl) = young leaves, (ml) = mature leaves.

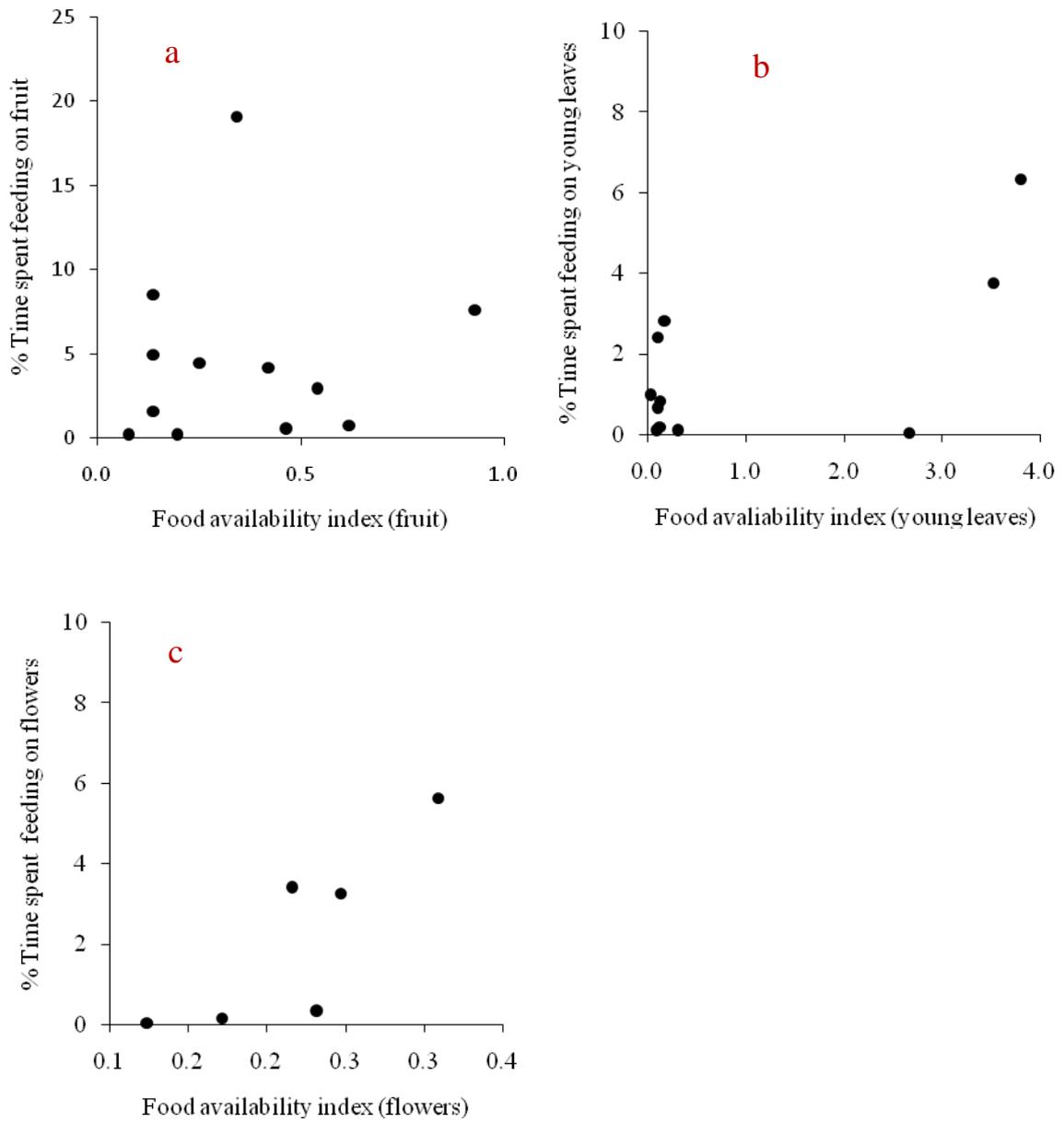


Figure 2.9: Scatter plots showing the relationship between (a) feeding time and $FAI_{(fr)}$, (b) feeding time and $FIA_{(yl)}$, (c) feeding on time and $FAI_{(fl)}$ from the top 10 species (the data was accumulated from the three-month study period, January, February and March 2015).

2.4 Discussion

2.4.1 Activity budgets

Activity budgets were similar between all members of the study group of northern yellow-cheeked crested gibbons (*N. annamensis*). This pattern is similar to other studies where individual primates in the same group spend similar amounts of time on each activity (Isbell & Young 1993; Fan *et al.* 2008; Frechette *et al.* in prep). This synchronous behaviour is relatively common when animals live in a group (Engel & Lamprecht 1997). This behaviour is also found in other gibbon studies, where when one member starts, others usually also join in (Islam & Feeroz 1992). The gibbons in group A spent the most activity time resting, followed by feeding and travelling. Socializing took up a comparatively minor part of the activity budget. This is similar to eastern hoolock gibbons (*Hoolock leuconedys*) that spend more time resting than other parts of their activity budgets (Fan *et al.* 2013). However, it contradicts another study where it was found that hoolock gibbons (*Hoolock hoolock*) spend most of their daily time feeding, particularly between October and April (Islam & Feeroz 1992). Although the present study did not analyse the various factors that influence this behaviour, other studies on gibbons and monkeys reveal that weather conditions including rainfall, temperature, and food availability may influence behaviour and may therefore be playing a role here (Islam & Feeroz 1992; Watanuki & Nakayama 1993; Fan *et al.* 2013).

During the study periods, selective illegal logging was occasionally observed, particularly in March, due to the lack of law enforcement during that time. Logging may modify the ecology and behaviours of some primate species due to the reducing food availability (Johns 1986; Hardus *et al.* 2012). After logging, orang-utans, spend more time travelling and searching for food (Hardus *et al.* 2012). Noise pollution, such as that produced by logging activities, also impacts animal behaviour (Hanson *et al.* 1976; Brumm 2004; Siemers & Schaub 2011). For example, while common marmosets (*Callithrix jacchus*) generally select habitats with high food availability (Pontes & Soares 2005), noise pollution, can lead to them avoiding such areas and instead selecting habitat with low levels of noise, even if there is low food availability in these areas (Duarte *et al.* 2011). Gibbons are territorial animals (Marshall & Marshall 1976), so their strategies of avoiding noise pollution may be different from other primates. The gibbons in group A were frequently out of observation or hiding when chainsaws were heard near the observation areas, compared to times when only researchers were present and the environment was quiet. They also

increased their inactive time when logging was more frequent (in March). This suggests that noise pollution from logging activities may modify the behaviour of *N. annamensis*, although future study is needed to clarify that how this behaviour will change when they are exposed to noise (logging or increased number of people).

2.4.2 Food plant selection

Although the two dominant plant species, *N. mutabile* and Nang Kmov (local name) are categorised by the local guides as gibbon feeding trees, they were not used as food sources during the study periods. The genus *Nephelium* normally bears fruit in late April and early May, and its fruit is also consumed by white-handed gibbons (*H. lar*) in Thailand (Whittington & Treesucon 1991). Although the gibbons selected 37 different plant species for their food sources, only 16 species (feeding more than 1%) were the most selected. However, the relative density of these most preferred food species (top 10 species) were very low inside the home range of this group of gibbons, particularly *I. umbellulata* and *Ficus. sp*, at 0.82% and 0.41%, respectively. This indicates that this group of *N. annamensis* actively selects rare over common plant species, at least at some points in the year. Since selective loggings and shifting cultivations are common near the study area, by cutting down those uncommon species would pose a serious threat to *N. annamensis*.

2.4.3 Diet budgets

Fruit makes up the majority of *N. annamensis*' diet. The gibbons mostly consumed only the flesh of the fruit, and generally spat seeds out, although some small fruits were swallowed with seeds. Other studies have also found that fruit is the main diet for most species in the Hylobatidae family (McConkey *et al.* 2002; Fan *et al.* 2013; Ni *et al.* 2014). However, in the harsh environment, some species of gibbons, *N. c. jingdongensis*, spend more time feeding on young leaves than fruit (Fan *et al.* 2009). Although fruit is important for *N. annamensis*, unripe fruit were usually avoided in the present study. The gibbons were not observed feeding on the unripe fruit from some species, including *W. edulis* and *M. elliptica*, and were rarely observed feeding on unripe fruit of *I. umbellulata*, *G. macrostachyum*, *Ficus. sp*, and *Ficus racemosa*. Similarly, white-handed gibbons (*H. lar*) consume only a small quantity of unripe fruit (Whittington & Treesucon 1991). This may be due to the fact that unripe fruits contain less sugar and lipids (Felton *et al.* 2009c), but higher concentration of toxins and other secondary compounds than ripe fruit (Wrangham & Waterman 1983).

Young leaves and flowers were also important plant tissues in the diet of this group of *N. annamensis*. The gibbons preferred the young leaves from *L. elegans* and the flowers from *D. alatus* over those of other plant species. Both young leaves and flowers from *G. oliveri* were also consumed by this study group. Mature leaves and insects including honey bee and bee larvae comprised the lowest proportion of the gibbons' diets. These feeding behaviours are also found in other gibbon species (Whittington & Treesucon 1991; McConkey *et al.* 2002; Fan *et al.* 2009; Borah *et al.* 2014). Together, these observations indicate that fruit is the preferred plant tissue in the diet of *N. annamensis*, and this is likely due to the fact that fruit has higher level of sugar and lipids than other plant parts (Rothman *et al.* 2006; Felton *et al.* 2009c). However, as with other gibbons, this gibbon species needs to consume alternative food sources in order to meet nutritional requirement including young leaves, which generally contain high concentration of protein (Rothman *et al.* 2006). Further details of the nutritional compositions of food consumed by *N. annamensis* see Chapter 3.

2.4.4 Food availability

Although *N. annamensis* spent most of the time feeding on fruit when it became available, there was no statistically significant relationship between feeding time and the availability of fruit (FAI_{fr}) inside the home range of this group of gibbons. This is due to the fact that only a small number of plants bore fruit, especially in January. Furthermore, the relative densities of trees and lianas that bore fruit were very low. For example, eight of the 10 most common food plants represented only ~7% of the total plant species, and only 3% of plants bore fruit in January, although the number increased to 10% in March (Figure 2.8). However, the small density of those plants produce a large abundance of fruit, which meant that the gibbons increased feeding time on fruit, but only in on small numbers of plant species.

There was also no significant relationship between feeding time and the availability of young leaves (FAI_{yl}). The absence of this relationship may be due to the fact that young leaves were an alternative food source for *N. annamensis*, as found in other studies (Fan *et al.* 2013; Ni *et al.* 2014). Most gibbons feed on fruit as the main diet, but may shift to young leaves or flowers during periods when fruit availability is low (McConkey *et al.* 2002; Fan *et al.* 2009; Mitrajit *et al.* 2014). The *N. annamensis* study group here spent more time feeding on young leaves in January, but this declined when fruit became available in March (Figure 2.7). However, there was a significant relationship between feeding time and availability of

flowers (FAI_{fl}). That is to say that time spent feeding increased when the species became more available in the habitat. The production of flowers in Cambodian forests mostly peak in February until April (Rawson 2009). Although flowers are a third choice for *N. annamensis*, there may be important nutrition values that this gibbon species need to include in their diets. Generally, individual flowers provide very low nutritional values, but flowers may serve as good sources of sugar, water content (Garber 1988) and minerals (Hladik 1977; Rop *et al.* 2012).

The present study clearly indicates that those small numbers of trees that bore fruit play an important role for gibbons' food sources during the study periods. The reason why the gibbons mainly select these 16 plant species for food sources is likely to be that they both produced a large quantity. This suggests that without special protection on those particular feeding plants, especially the 10 feeding plant species, there may be a negative effect on the population size of this gibbon species. The reduction of food availability may affect the lifespan and reproductive success of this species as it does for other primates (Thompson & Wrangham 2008; Mattison *et al.* 2012). Because of the removal of trees in Uganda, the population size of the olive baboon (*Papio anubis*) and common chimpanzee (*Pan troglodytes*) were lower in logged forested areas than non-logged forested areas (Plumptre & Reynolds 1994). Juvenile and infant primates in selectively logged regions generally have higher mortality rates than those in non-logging habitats (Chapman *et al.* 2000). This may due to the fact that those primates consumed food with lower nutritional values due to the deduction of food availability, leading to the overall consumption of lower quality and lower milk production by lactating females (Altmann *et al.* 1977).

2.5 Summary

All *N. annamensis* individuals in the study group spent similar amounts of time on each activity in their activity budget, and fed on similar plant tissues. They spent most of the time resting compared to other activities, including feeding, travelling and socializing. Although the gibbons spent more time feeding on flowers when they became available, no relationships were found between feeding time and availability of fruit or young leaves. Fruit is a staple diet of this gibbon species, but they also consumed young leaves, flowers, mature leaves, and insects as alternative food sources. Although *N. annamensis* selected 37 plant species as food sources, 16 of these plant species contributed a major role in their diets. Of these 16 important food plant species, only a few of them bore a large amount of fruit during the study period in particular, *I. umbellulata*, *Ficus. sp.*, and *W. edulis*. These species were particularly important food sources for *N. annamensis*; however, their relative density was very low inside the home range of this group of gibbons.

These results clearly indicate that this gibbon species selected rare over common plant species for food. These findings contribute to long-term conservation programs for this species in the wild, by suggesting key food species (*I. umbellulata*, *Ficus. sp.*, *L. elegans*, *G. oliveri* and *W. edulis*) which should be additionally protected. The availability of preferred food species must be maintained, lest a reduction in food availability reduce population sizes of primates (Plumptre & Reynolds 1994; Chapman *et al.* 2000; Thompson & Wrangham 2008; Duarte *et al.* 2011). Other factors that may have influenced the behavioural ecology of this species were logging and noise pollution. Although data is currently insufficient to show whether noise pollution from chainsaws influences the behavioural ecology of *N. annamensis*, future studies are needed, as it does affect other primate species (Pontes & Soares 2005; Hardus *et al.* 2012) and may appear to impact the behaviour of *N. annamensis*.

Chapter 3

Nutritional composition of northern yellow-cheeked crested gibbons (*Nomascus annamensis*) diets in northern Cambodia

3.1 Introduction

Food is the most important resource for all living organisms (Leibold & Wilbur 1992; Mead *et al.* 1999; Grandison *et al.* 2009), as it can affect health, lifespan, social relationships, fitness and reproduction (Fernandes *et al.* 1976; Koenig *et al.* 1997; Givens & Shingfield 2004; Grandison *et al.* 2009; Harris *et al.* 2010; Trepanowski *et al.* 2011). In order to optimise the benefits of food items, animals must make a choice about which foods to include in their diets (Felton *et al.* 2009c; Matsuda *et al.* 2013). Optimal foraging theory states that animals will maximize nutritional intake while minimising searching time in order to conserve energy (MacArthur & Pianka 1966; Cowles *et al.* 1988; Demott 1989; Belovsky 1997). Following this theory, it would be expected that to maximize nutritional intake, most animals would select high quality food sources (those with easily digestible nutrients) over those of lower quality (that are harder to digest) (Milton 1979; Cowles *et al.* 1988; Moser *et al.* 2006). In addition, most animals should search for food in areas of high food availability (Vedder 1984; Moser *et al.* 2006), and increase resting time when food is less available (Watanuki & Nakayama 1993; Korstjens *et al.* 2010). These ideas have led to research on food selection (MacArthur & Pianka 1966; Mckey *et al.* 1981; Kool 1992; Belovsky 1997; Chapman & Chapman 2002), and the role of plant chemistry in food selection by animals (Speiser & Rowell-Rahier 1991; Coley & Barone 1996; Rothman *et al.* 2006; Felton *et al.* 2009a; Behie & Pavelka 2012a).

Research on primates has found that many primate species prioritise plant foods with high concentrations of protein (Milton 1979; Rothman *et al.* 2008b; Felton *et al.* 2009a; Felton *et al.* 2009b; Felton *et al.* 2009c; Rothman *et al.* 2011; Hanya & Bernard 2015). This is due to the fact that protein is a crucial nutrient for reproduction, growth, and survival (Mattson Jr 1980; Yiming 2006; Felton *et al.* 2009a; Felton *et al.* 2009b). However, different species of primates rely on different sources for protein. For example, most gibbons (Hylobatidae) normally gain protein from protein-rich insects rather than plant tissues (Chivers 1998; Borah *et al.* 2014), whereas the Old World colobines consume young leaves as their main source of protein (Kool 1992; Chivers 1998; Chapman & Chapman 2002). Even

for species that ingest primarily low protein fruit, some groups have been found to maintain a consistent daily protein intake, while allowing the relative intake of other nutrients including lipids and carbohydrates (sugar and starch) to fluctuate (Felton *et al.* 2009c), showing the importance of protein selection for all species regardless of diet type.

Plant tissues with a high fibre content and/or high levels of secondary compounds tend to be less selected or avoided by most primate species (Davies *et al.* 1988; Yiming 2006; Hanya & Bernard 2015). This is perhaps to be expected, considering that food items with high concentrations of secondary metabolites are difficult to digest, lack nutritional value, and can contain toxins (Glander 1982; Davies *et al.* 1988; Chapman & Chapman 2002; Acamovic & Brooker 2005; Simmen *et al.* 2013). For example, unripe fruits are usually avoided by white-handed gibbons (*Hylobates lar*) (Whittington & Treesucon 1991). This may be because unripe fruit not only contain less sugar and lipids (Felton *et al.* 2009c), but also have higher concentrations of toxins and other secondary compounds than ripe fruit (Wrangham & Waterman 1983). Similarly, mature leaves are normally avoided by most primates (Kool 1992; Felton *et al.* 2009c). However, in contrast to usual primate food-selection behaviour, black howler monkeys (*Alouatta pigra*) preferentially select mature leaves over young leaves following a hurricane in 2001, due to the higher concentration of simple sugars (Behie & Pavelka 2012a). These variable findings suggest that the composition of primate diets are complicated and highly dependent on species and the environments in which they are found (Chapman & Chapman 2002; Strier 2007; Smith *et al.* 2013).

Nutritional geometry has recently been proposed as a framework to simplify the complexity of primate nutritional ecology (Simpson & Raubenheimer 1995; Raubenheimer 2011). A nutritional geometrical framework (GF) is used to show those nutrients that are prioritized by animals, and those that are allowed to fluctuate (Simpson & Raubenheimer 1993; Raubenheimer & Simpson 1997). This model has been tested in some primate species including mountain gorillas (*Gorilla beringei*) (Rothman *et al.* 2011) and Peruvian spider monkeys (*Ateles chamek*) (Felton *et al.* 2009c). While this method provides a more accurate picture of food selection in wild primates, it does require detailed measurements of the amount of each food item consumed, which often precludes its use (Raubenheimer *et al.* 2015). The right-angled mixture triangle (RMT) is a simpler method that uses the variation in dietary nutrients as a proportion rather than overall amount in a single graph (Figure 3.1) (Raubenheimer 2011; Raubenheimer *et al.* 2015). The RMT model provides data on an animal's food selection, mixture of food items, and nutritional requirements (Raubenheimer

2011), enabling simple and effective comparisons between species or populations, and annual intakes of nutritional components consumed primates, including protein, lipid, and fibre (Raubenheimer *et al.* 2015). Consequently, the RMT model is a useful and appropriate tool when comparing food selection and nutritional requirements, and this model has been tested in some primate species, including chacma baboon (*Papio hamadryas ursinus*) (Johnson *et al.* 2013), common chimpanzees (*Pan troglodytes*), blue monkeys (*Cercopithecus mitis*), red-tailed monkeys (*Lophocebus albigena*), grey-cheeked mangabey (*Lophocebus albigena*) and mountain gorillas (*G. beringei*) (Raubenheimer *et al.* 2015).

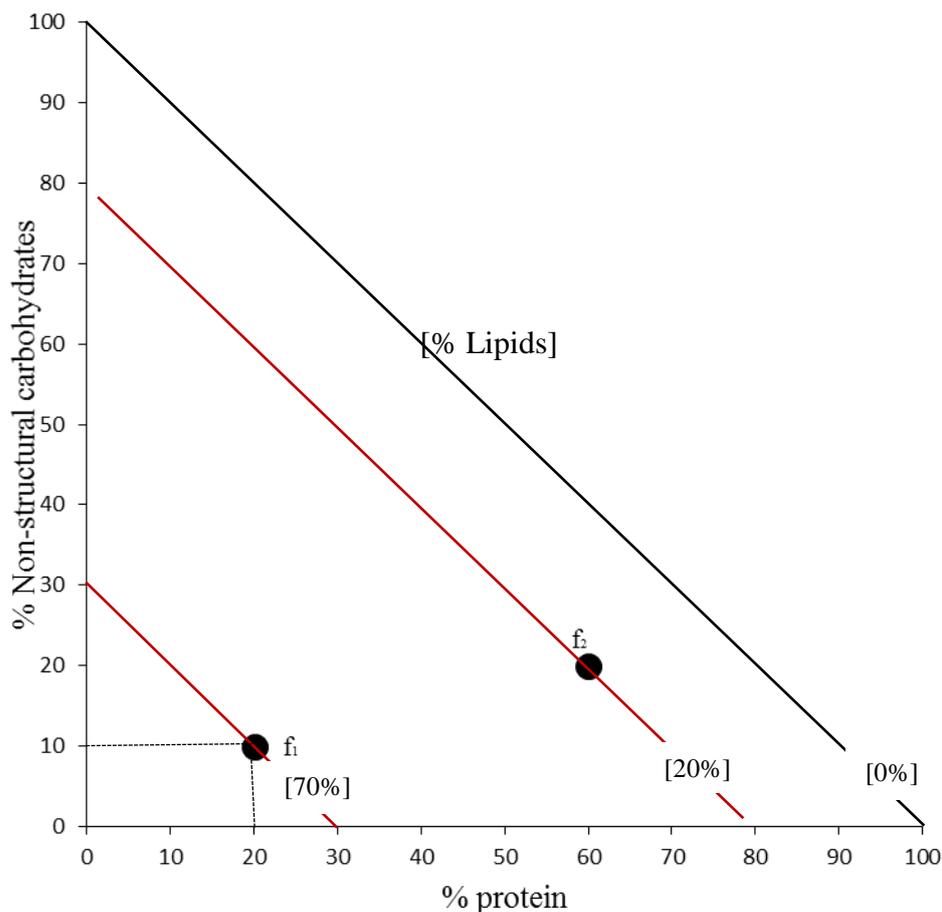


Figure 3.1: An example of right-angled mixture triangle (RMT) showing the combination of protein (P), total non-structural carbohydrates (TNC) and lipids (L) of two food items (f_1 and f_2). P and TNC are plotted on the X and Y axes, respectively. The lipid (L) content is determined by the equation $L = 100 - (TNC + P)$, assuming the total value of P, TNC, and L are 100%. The values of L are illustrated by a series of diagonal lines. Each point (f_1 and f_2) represents the percentage of P, TNC, and L in each food item. For example, f_1 contains 20% P and 10% TNC, so the value of L is $100 - (20 + 10) = 70\%$. So, to gain more lipids, animals need to eat f_1 , or any food item that fits on the 70% L diagonal line. Food item f_2 , is on the 20% lipid line with 60% P and 20% TNC.

Source: Modified from Raubenheimer *et al.* (2015)

Despite the recent use of GF and RMTs in primate studies, current knowledge of the drivers of food selection in these animals remains limited (Rothman *et al.* 2006; Rothman *et al.* 2008b; Felton *et al.* 2009a; Felton *et al.* 2009c; Behie & Pavelka 2012b; Simmen *et al.* 2013), with relatively nothing known regarding crested gibbons (*Nomascus. spp*). Crested gibbons are among the most endangered primates in the world (Geissmann 2007). Populations of these species have declined significantly due to habitat destruction and hunting (Cheyne *et al.* 2008; Gray *et al.* 2010; Rawson 2010b). Most species of crested gibbons are listed as Endangered or Critically Endangered by the IUCN Red List and all are in CITES Appendix I (Geissmann 2007; Rawson 2010b). The northern yellow-cheeked crested gibbon (*Nomascus annamensis*) is a newly described species (Thinh *et al.* 2010) and even though the status of this species has not yet been updated, it is likely to be listed as Endangered by IUCN Red List as it faces similar threats to other gibbons (Thinh *et al.* 2010).

Fruit is the main diet of *N. annamensis*, supplemented with young leaves, flowers, mature leaves and insects (Frechette *et al.* in prep; Chapter 2) However, the nutritional composition of these food items is as yet unknown. This knowledge would allow an understanding of the nutritional requirements of this endangered species. This understanding would also help policy makers to preserve key food resources for wild populations. Monitoring key plant species would then help maintain wild gibbon populations by protecting crucial resources for the survival of these animals. In focussing on food selection by *N. annamensis* and detailing the nutritional composition and value of food items ingested by this species, this study will contribute to long-term primate conservation programs, not only in Cambodia, but in other countries where this gibbon species is found. As such, this chapter focuses on the drivers of food selection in *N. annamensis* in northern Cambodia, and aims to answer two basic questions: (1) What are the nutritional compositions of food items selected by this gibbon species? (2) Using the RMT model (Raubenheimer *et al.* 2015), what food items and nutritional compositions are targeted by this group of *N. annamensis*?

3.2 Methods

See Chapter 2 sections 2.2.1, 2.2.2, and 2.2.3 for details of the study site, study group of *N. annamensis*, and behavioural data collection, respectively.

3.2.1 Plant sample collection

Where possible, samples of food items (plant tissues) were obtained from trees and lianas on the same day as gibbons were observed feeding on them. If samples could not be obtained immediately, the plant was tagged with a coloured tag, its GPS location noted, and it was climbed the next day, with assistance from local villagers when required (Figure 3.2). Samples were collected from as close a location as possible within the tree or liana to where the gibbon had been seen feeding. Fruit samples were collected at a similar level of ripeness to those consumed, and leaves and flowers (Figure 3.3a) of a similar age were selected. If the observed feeding area was too high for samples to be safely collected, plant samples were collected from trees or lianas of the same species nearby or inside the home range of the study group.

Once back at base camp, each sample was weighed on a balance until the final mass was 100 ± 0.1 g. Before weighing, food items were processed as the gibbons processed them. For example, seeds were removed from any fruit samples if the gibbons did not eat the seeds (Figure 3.3b). Samples were air-dried in direct sunlight (between 7 and 15 days or until the dry weight was constant), and then re-weighed to give an initial dry weight. Samples were then sealed in plastic bags and stored out of sunlight. One bag of silica gel was put in each bag of plant sample to absorb any moisture and avoid decomposition. Samples were then exported for analysis at the Nutritional Ecology Lab at Hunter College, the City University of New York (CUNY), USA where they were stored at room temperature until analysis.



Figure 3.2: Plant sample collection. Most samples were collected by climbing. (a) Local assistant climbing *I. umbellulata* to collect fruit samples; (b) selecting fruit samples after collection. The ripe fruit from this species are red, yellow, and slightly yellow, while the unripe fruits are green and dark green.

Photo: Nave Hon and Noy Gnet.



Figure 3.3: Plant sample preparation. Flowers of *D. alatus* were (a) collected at the field site, and (b) seeds of *M. elliptica* were removed, in preparation for drying in direct sunlight. The ripe fruit from this species are yellow or slightly green and yellow, while the unripe fruits are green and dark green.

Photo: Naven Hon

3.2.2 Nutritional analyses

The nutritional analyses of all plant samples were undertaken at the Nutritional Ecology Lab at Hunter College with the assistance of Dr Jessica Rothman's team. Seventy-four plant samples (plant tissues) from 20 plant species were selected for analysis. The samples were comprised of 66 trees, six lianas, and two epiphytes and included fruit ($N = 39$), young leaves ($N = 15$), flowers ($N = 14$), and mature leaves ($N = 6$). All plant samples were ground in a Wiley Mill[®] (Arthur H. Thomas Co., Philadelphia, PA), and passed through a 1-mm screen (Rothman *et al.* 2006). The samples were analysed for protein (P), lipids (L), total non-structural carbohydrate (TNC), neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL), and the presence and absence of condensed tannins in dry matter (DM). Before analysis, samples were oven-dried at 105°C to obtain the absolute DM of the samples.

The moisture content was determined from the fresh weight (FW) and dry weight (DW) of the sample. Protein was calculated through combustion analysis using Leco Tru Spec nitrogen (N) analyser by calculating $N \times 6.25$ to get protein (Licitra *et al.* 1996; Rothman *et al.* 2008a), and followed the protocol of Licitra *et al.* (1999). A method of analysing lipids was adapted from ANKOM Technology, and followed the protocol of Rothman *et al.* (2012). The cellulose and hemicellulose of the plant samples were measured via NDF, ADF, and ADL (Van Soest *et al.* 1991; Rothman *et al.* 2006). NDF includes both ADF and lignin, and it contains cellulose, hemicellulose and lignin, while ADF contains cellulose and lignin (Van Soest *et al.* 1991; Rothman *et al.* 2006; Rothman *et al.* 2012). The amount of ADL is estimated by removing cellulose and residual ash (Rothman *et al.* 2006). Finally, TNC was calculated by subtracting all other nutrients including crude protein, NDF, ash, and lipids from all plant samples (Rothman *et al.* 2012). Condensed tannins were estimated using an acid-butanol assay (Porter *et al.* 1985). A qualitative system was used to report the presence and absence of condensed tannins by measuring the absorbance values at 0.10 – 0.50 (+), 0.50-1.00 or above (++), 1.00, while values lower than 0.10 were marked as absent (Rothman *et al.* 2006).

3.2.3 Statistical analyses

The data were non-normal distributed, so Kruskal-Wallis tests were used to compare between groups (more than 2 groups), while Mann-Whitney U tests were used to conduct

pairwise tests. The percentage of nutrients (P, L, and TNC) and the concentration of different types of fibres (NDF, ADF, and ADL) of each plant tissue (fruit, flowers, young leaves and mature leaves) were compared using Kruskal-Wallis tests. Mann-Whitney *U* tests were used to compare moisture, P, L, TNC, NDF, ADF, and ADL in each plant tissue.

A right-angled mixture triangle (RMT) (Raubenheimer *et al.* 2015) was then constructed to show the relative contribution of P, TNC and L in each food item in a single plot. Sixty-nine samples from 19 plant species were used for this model, including fruit ($N = 34$), flowers ($N = 14$), young leaves ($N = 15$) and mature leaves ($N = 6$). Another five fruit samples were excluded from the analyses because some nutritional data was not available. The Kruskal-Wallis tests were used to compare the overall nutritional compositions (P, TNC and L) in the 74 food samples [Food item f_{10} (Kbal Thum) was excluded in the analyses because protein data was unavailable]. Mann-Whitney *U* tests were used to compare differences in P, L, and TNC in all 74 food samples.

All statistical analyses were performed in SPSS version 22, and in most cases $\alpha = 0.05$. In pairwise tests (Mann-Whitney *U* tests), a Bonferroni correction ($0.05/N$, i.e., $\alpha = 0.0125$) was used to adjust for multiple tests (Rice 1989).

3.3 Results

3.3.1 Nutritional composition of *Nomascus annamensis* diets

The nutritional composition of each plant tissue sample consumed by the study group of *N. annamensis* is summarised in Table 3.1. Seventy-four plant samples from the 20 plant species consumed by this group of gibbons were collected for nutritional analyses including P, L, TNC, fibres (ADL, ADF, and NDF) and condensed tannins (Table 3.2).

Table 3.1: Mean amount of nutrients (% dry matter) in plant tissues consumed by one habituated group of northern yellow-cheeked crested gibbons (*N. annamensis*) from January – April 2015 at Veun Sai-Siem Pang Conservation Area (VSSPCA), Cambodia.

Plant tissues	N	Mean (%)	SD	Plant tissues	N	Mean (%)	SD
Fruit				Young leaves			
Moisture*	39	69.52	11.92	Moisture	15	80.34	4.06
Protein	34	8.76	3.79	Protein	15	22.45	6.93
TNC	34	40.24	13.54	TNC	15	26.66	11.11
Lipids	34	5.64	4.57	Lipids	15	2.48	2.27
Ash	34	5.86	3.62	Ash	15	6.78	4.54
NDF	34	39.50	12.56	NDF	15	41.63	8.96
ADF	34	31.32	11.24	ADF	15	28.34	12.35
ADL	34	18.74	6.88	ADL	15	25.73	10.19
Flowers				Mature leaves			
Moisture	14	79.46	2.97	Moisture	6	88.93	4.16
Protein	14	9.39	2.87	Protein	6	6.22	3.56
TNC	14	38.54	10.76	TNC	6	31.30	7.19
Lipids	14	5.98	3.89	Lipids	6	5.00	3.44
Ash	14	4.50	1.75	Ash	6	13.42	4.19
NDF	14	41.59	8.69	NDF	6	44.06	7.92
ADF	14	30.81	12.56	ADF	6	37.86	14.86
ADL	14	28.61	7.85	ADL	6	18.48	4.74

SD: Standard deviation, TNC: total non-structural carbohydrates, ADL: acid detergent lignin, ADF: acid detergent fibre, NDF: neutral detergent fibre. In the fruit section, the samples sizes for moisture* was $N = 39$, because the data for one sample was not available. The sample sizes for other nutritional compositions of fruit was $N = 34$, because nutritional data for six samples were not available.

Table 3.2: Mean nutritional compositions (% dry matter) from the 20 plant species (trees and lianas) consumed by the northern yellow-cheeked crested gibbons (*N. annamensis*) from January – April 2015 at VSSPCA, Cambodia.

Food	Species	N	Life form	Part	%H ₂ O	%Protein	%Lipids	%TNC	Ash%	%NDF	%ADF	%ADL	Tannins
f1	<i>Aglaia grandis</i>	1	Tree	Fr	82.53	6.26	4.10	59.24	8.38	22.02	19.21	14.95	0
f2	<i>Dialium cochinchinensis</i>	4	Tree	YL	77.67	20.06	1.87	31.68	2.76	43.63	22.42	27.85	+
f3	<i>Dipterocarpus alatus</i>	7	Tree	Fl	79.42	7.20	3.02	43.72	4.07	41.99	35.97	28.91	0
f4	<i>Dischidia ruscifolia</i>	2	Epiphyte	ML	91.54	3.45	3.04	29.50	16.20	47.82	44.95	19.99	0
f5	<i>Dischidia. Sp</i>	2	Epiphyte	ML	91.65	4.46	3.28	27.10	15.10	50.07	48.41	17.00	0
f6	<i>Ficus. Sp (2)</i>	10	Liana	Fr	60.29	5.23	2.40	33.09	7.03	52.25	38.93	27.74	0
f7	<i>Garcinia oliveri (4)</i>	5	Tree	Fl	81.22	11.71	10.92	30.65	4.78	41.94	28.75	27.74	+
f7	<i>Garcinia oliveri</i>	2	Tree	YL	88.02	16.07	2.99	40.14	5.90	34.90	18.97	18.51	0
f8	<i>Gnetum macrostachyum</i>	5	Liana	Fr	49.65	12.75	1.87	38.36	1.87	45.15	24.03	20.98	0
f9	<i>Ilex umbellulata (1)</i>	1	Tree	Fl	71.64	7.68	5.49	47.79	6.85	32.18	11.53	23.66	++
f9	<i>Ilex umbellulata (1)</i>	12	Tree	Fr	74.81	11.67	9.20	41.09	7.13	30.91	19.80	18.65	+
f10	Kbal Thum (LN)	2	Tree	Fr	74.62	ND	22.21	ND	5.80	44.41	24.14	11.74	0
f11	<i>Lithocarpus elegans (3)</i>	2	Tree	YL	83.25	32.99	1.90	27.95	7.96	29.20	15.77	15.35	0
f12	<i>Madhuca elliptica**</i>	4	Tree	Fr	75.97	5.03	5.52	58.11	4.61	36.69	36.48	26.75	0
f13	<i>Mangifera duperreana</i>	2	Tree	YL	75.05	23.91	1.80	9.00	9.79	55.49	45.64	44.99	0
f14	<i>Ochna atropurpurea</i>	1	Tree	YL	78.82	23.53	0.60	25.21	6.95	43.71	33.89	25.04	++
f14	<i>Ochna atropurpurea</i>	1	Tree	Fl	78.75	14.76	2.55	32.48	3.78	46.43	24.30	38.26	0
f15	<i>Syzygium. Sp</i>	1	Tree	YL	79.48	10.40	1.80	41.89	5.67	40.24	37.31	26.91	+
f16	<i>Unknown Liana</i>	1	Liana	YL	80.04	30.92	2.67	8.42	19.9	38.06	26.64	12.64	0
f17	Vor Chrey Sleptom (LN)	2	Liana	ML	83.60	10.77	8.69	37.30	8.97	34.28	20.21	18.46	+
f18	Vor Krovanh (LN)	1	Liana	YL	80.48	30.54	10.26	20.87	5.47	32.86	29.82	25.73	0
f19	Vor Tangant (LN)	1	Liana	YL	82.88	15.09	1.05	22.68	5.37	55.80	47.02	26.55	0
f20	<i>Willughbeia edulis (5)</i>	5	Liana	Fr	83.36	3.97	6.65	64.24	2.03	26.86	22.43	18.54	+

Key: YL: young leaves, ML: mature leaves, Fl: flowers, Fr: fruit, LN: local name, TNC: total non-structural carbohydrate, ADL: acid detergent lignin, ADF: acid detergent fibre, NDF: neutral detergent fibre, ND: no data. Condensed tannins absorbance values represent absorbance units of 0.10-0.50 (+), 0.50-1.00 (++) in a 12.5 mg/ml solution (dry weight) of plant sample. The number in brackets in the species column is the ranking of the top 5 plant species, order from 1 to 5, from the highest percentage of time spent feeding on a species (1) to the highest (5).

3.3.1.1 Moisture

Overall, moisture content was significantly different between all plant tissues (Kruskal-Wallis test: $H = 31.34$, $P = 0.0001$; Figure 3.4), fruit and flowers (Mann-Whitey tests: $U = 114$, $P = 0.001$), fruit and young leaves ($U = 107$, $P = 0.0001$), fruit and mature leaves ($U = 3$, $P = 0.0001$), flowers and mature leaves ($U = 1$, $P = 0.001$), and young leaves and mature leaves ($U = 5$, $P = 0.002$). Only flowers and young leaves were similar ($U = 101$, $P = 0.86$). Fruit had the lowest moisture content (69.52%), while mature leaves contained more water (88.93%) than young leaves (80.34%), and flowers (79.46%) (Figure 3.4). *N. annamensis* drank water from cavities within tree trunks (Appendix 2, Figure 3), and were never seen drinking water from the ground.

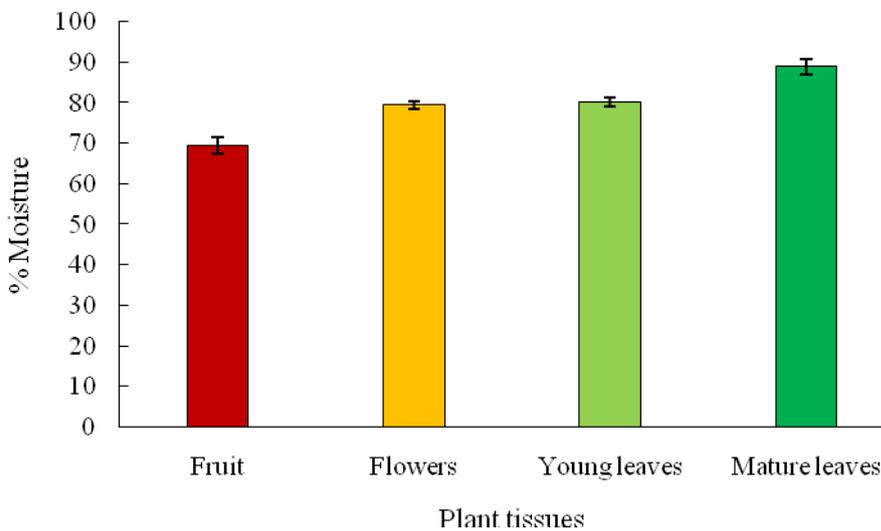


Figure 3.4: The average percentage of moisture contents in food items (fruit, flowers, young leaves and mature leaves) eaten by the study group of *N. annamensis* (\pm standard error).

3.3.1.2 Protein

Generally, the concentration of protein was significantly different among each plant tissue type (Kruskal-Wallis test: $H = 33.61$, $P = 0.0001$; Figure 3.5). Young leaves contained more protein than fruit (Mann-Whitney test: $U = 14$, $P = 0.0001$), flowers ($U = 2$, $P = 0.0001$) and mature leaves ($U = 2$, $P = 0.002$), while the protein content of other plant tissues were not statistically different from each other (all: $P \geq 0.10$). Young leaves had the highest level of protein (22.45%), followed by flowers (9.39%), fruit (8.52%), and mature leaves (6.22%) (Figure 3.5).

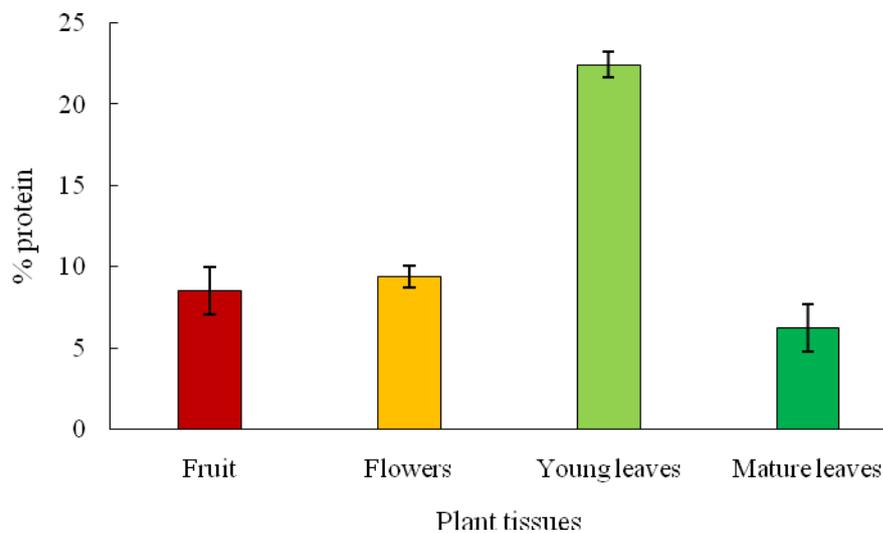


Figure 3.5: The average percentage of protein levelsof food items (fruit, flowers, young leaves and mature leaves) eaten by the study group of *N. annamensis* (\pm standard error).

3.3.1.3 Lipids

Overall, the amount of lipids was significantly different for all plant tissues (Kruskal-Wallis test: $H = 31.34$, $P = 0.005$; Figure 3.6). Young leaves had significantly lower lipid levels than fruit (Mann-Whitey tests: $U = 140$, $P = 0.002$) and flowers ($U = 24$, $P = 0.0001$), while the lipid contents of other food items were similar: fruit and flowers ($U = 244$, $P = 0.47$), fruit and mature leaves ($U = 109$, $P = 0.72$), flowers and mature leaves ($U = 36$, $P = 0.62$) and young and mature leaves ($U = 23$, $P = 0.08$). Fruit had the highest level of lipids (6.70%), while flowers and mature leaves contained 5.98% and 4%, respectively, and young leaves (2.48%) had the lowest (Figure 3.6).

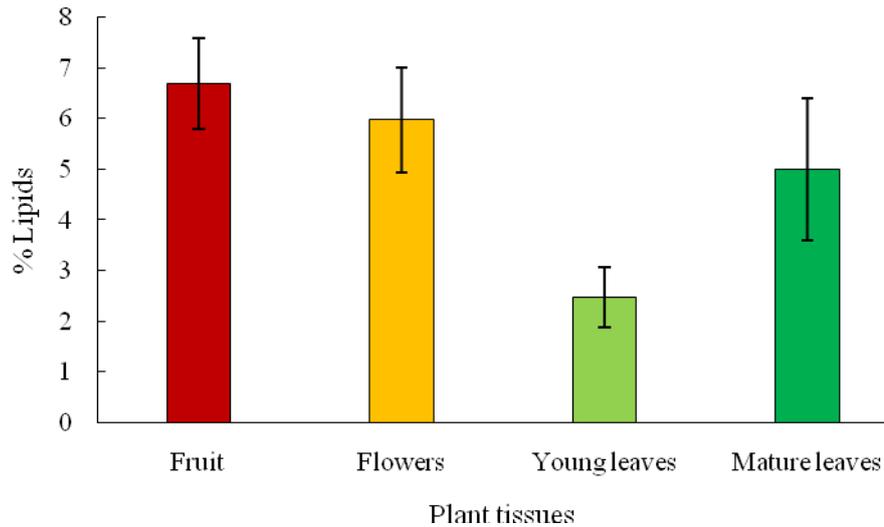


Figure 3.6: The average percentage of lipid levels of food items (fruit, flowers, young leaves and mature leaves) eaten by gibbons in the study group of *N. annamensis* (\pm standard error)

3.3.1.4 Total non-structural carbohydrates (TNC)

Generally, the level of TNC was significantly different among all plant tissues (Kruskal-Wallis test: $H = 15.3$, $P = 0.002$; Figure 3.7). Upon pairwise analysis, significant differences were found between the TNC content of fruit and young leaves (Mann-Whitey tests: $U = 91$, $P = 0.0001$) and flowers and young leaves ($U = 49$, $P = 0.01$). All other pairwise comparisons yielded no statistically significant results (all: $P \geq 0.04$). Fruit had the highest concentration of TNC (42.59%), while flowers, mature leaves and young leaves contained 38.54%, 31.00%, and 26.66%, respectively (Figure 3.7).

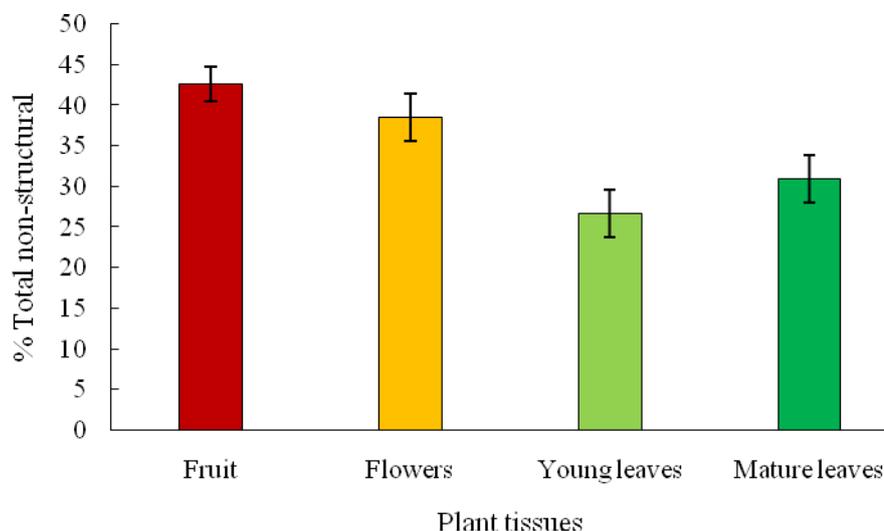


Figure 3.7: The average percentage of total non-structural carbohydrates of food items (fruit, flowers, young leaves and mature leaves) eaten by the study group of *N. annamensis* (\pm standard error).

3.3.1.5 Fibre

Overall, there was no difference in the amount of NDF (Kruskal-Wallis test: $H = 1.42$, $P = 0.69$), ADF ($H = 3.46$, $P = 0.32$), or ADL ($H = 6.83$, $P = 0.07$) among all plant tissues consumed by this group of gibbons (Figure 3.8). All pairwise comparisons revealed no significant differences between plant tissue types (Table 3.3 and Figure 3.8).

Table 3.3: Result of Mann-Whitney U tests for pairwise comparison of NDF, ADF and ADL in plant tissues consumed by the northern yellow-cheeked crested gibbons in group A.

Plant tissues	NDF		ADF		ADL	
	U	P	U	P	U	P
Fruit and flowers	248	0.7	207	0.2	155	0.02
Fruit and young leaves	253	0.5	246	0.4	246	0.4
Fruit and mature leaves	93	0.5	57	0.05	84	0.3
Flowers and young leaves	85	0.4	78	0.2	84	0.4
Flowers and Mature leaves	27	0.2	22	0.1	16	0.03
Young leaves and mature leaves	36	0.5	30	0.2	30	0.2

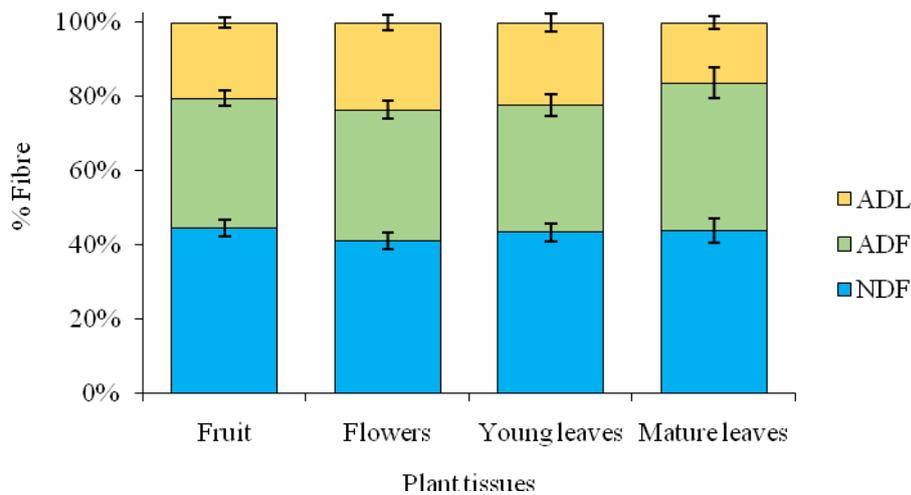


Figure 3.8: The average percentage fibre content of acid detergent lignin (ADL), acid detergent fibre (ADF), and neutral detergent fibre (NDF) of food items (fruit, flowers, young leaves and mature leaves) eaten by the study group of *N. annamensis* (\pm standard error).

3.3.1.6 Condensed tannins

Thirty-two percent of all plant tissues selected by this gibbon group contained condensed tannins. Flowers contained more often condensed tannins than other plant tissues. While some plant tissues contained condensed tannins and others did not, overall there were no significant differences between plant tissues (Kruskal-Wallis test: $H = 0.32$, $P = 0.95$). Similarly, pairwise comparisons of each plant tissue showed no significant differences (all: $P \geq 0.56$). Forty-three percent of flowers consumed by *N. annamensis* contained condensed tannins, while 33% of mature leaves, 30% of fruits, and 27% of young leaves contained tannins (Table 3.2).

3.3.2 Balance of nutrients in foods eaten by *Nomasus annamensis*

There were statistically significant differences in the relative content of TNC, P, and L in food items selected by *N. annamensis* (Kruskal-Wallis test: $H = 146$, $P = 0.0001$). Pairwise tests showed that the group of *N. annamensis* studied here consumed food items with significantly more TNC than protein (Mann-Whitey tests: $U = 173.5$, $P = 0.0001$) and lipids ($U = 7$, $P = 0.0001$). Similarly, they consumed food items with significantly more protein concentration than lipids ($U = 740$, $P = 0.0001$). Those food items were among the top plant species selected by *N. annamensis* particularly high in TNC (Figure 3.9, Table 3.1). For example, two frequently ingested food items had the highest concentration of TNC relative to P and L: *M. elliptica* (f₁₂, fruit, TNC: 89.32%, P: 7.71%, L: 2.97%); and *W. edulis*,

f₂₀, fruit, TNC: 87.09%, P: 5.38%, L: 7.53%). Some food items were notable for a comparatively low levels of TNC and L but high P levels; an unknown liana (f₁₆, young leaves, P: 73.61%, TNC: 20.04%, L: 6.35%) and *M. duperreana* (f₁₃, young leaves, P: 69.13%, TNC: 25.80%, L: 5.07%). All food items analysed were low in L relative to TNC and P (Figure 3.9).

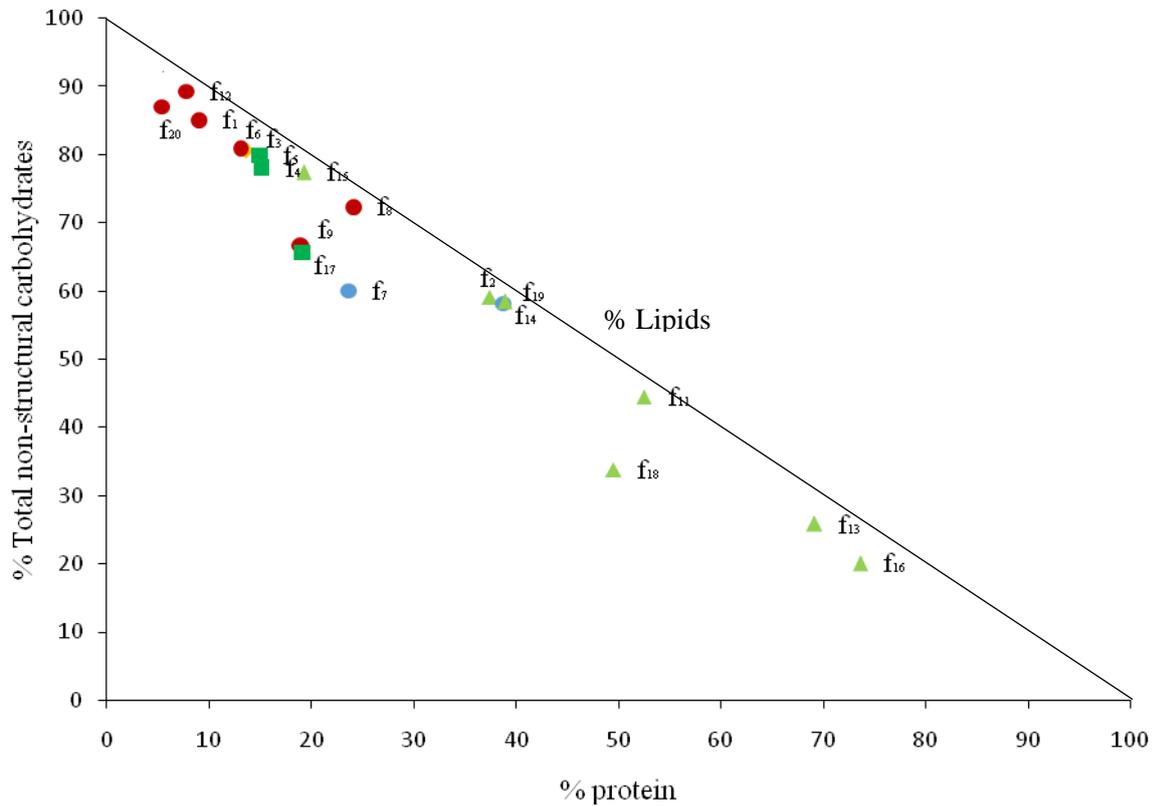


Figure 3.9: Right-angled mixture triangle (RMT) showing the relative contribution of total non-structural carbohydrates (TNC), protein (P) and lipids (L) of food items from particular plant species consumed by the northern yellow-cheeked crested gibbon (*N. annamensis*) at Veun Sai-Siem Pang Conservation Area (VSSPCA), northern Cambodia. P and TNC are plotted on the X and Y axes respectively, while L is depicted on the diagonal. Each point (f₁...f₂₀) represents the average energy mixture provided by the food item from that plant species, e.g. f₂₀ is a fruit (*W. edulis*) that supplies 87.14% energy from TNC, 5.85% from protein and 7% from lipids. The red circles are fruit, light-green triangles are young leaves, dark-green squares are mature leaves, orange diamonds are flowers, and blue circles are species where both flowers and young leaves were consumed.

Note: Food code from f₁ until f₂₀ see the first column of Table 3.2.

3.4 Discussion

3.4.1 Nutritional composition of plant tissues

Each type of plant tissue consumed by *N. annamensis* had different nutritional compositions. Fruit, the principal food source for these gibbons (60.36% in diet, Chapter 2), had the highest levels of TNC and lipids. Mature leaves had the highest moisture content, while young leaves had the highest concentration of protein, and flowers contained more often condensed tannins than other plant tissues. All plant tissues consumed by this group of gibbons had similar amounts of NDF, ADF, and ADL.

The group of *N. annamensis* were never seen drinking water from sources on the ground. During the period of this study (dry season), they were only observed drinking water from the cavities within tree trunks. However, considering the high moisture content of mature leaves found in this study, mature leaves may be acting as another water source for this group during the dry season. A similar result was found in mountain gorillas (*G. beringei*), that consume pith, which has low nutritional value but is high in moisture (Rothman *et al.* 2006), when water availability is low. While mature leaves are generally avoided by primates due to their high fibre content and the associated difficulty in digestion (Milton 1979; Davies *et al.* 1988; Kool 1992), this did not seem to be an obstacle here; mature leaves selected by *N. annamensis* had surprisingly similar fibre levels to other ingested food items. Coupled with their high moisture content, they may be valuable to these gibbons' diets during the dry season.

It is likely that this group of gibbons gain most of their protein by consuming young leaves (Figure 3.5) as do most primates living in natural habitats (Milton 1979; Milton 1999; Rothman *et al.* 2006; Irwin *et al.* 2014). This contradicts other gibbon studies that report that insects serve as protein sources (Chivers 1998; O'Malley & Power 2012; Borah *et al.* 2014; Rothman *et al.* 2014). While young leaves may also contain other nutritional compounds including lipids and primates generally consume young leaves primarily to meet their protein requirements (Milton 1979; Oftedal *et al.* 1991; Felton *et al.* 2009a; Felton *et al.* 2009b; Rothman *et al.* 2011). In this study, young leaves contained significantly more protein than other ingested plant items, suggesting that *N. annamensis* individuals also consume young leaves to meet their protein requirements. However, future studies are need to estimate the nutritional contribution of insects to the diet of *N. annamensis*.

Fruit was a major source of carbohydrates for *N. annamensis*. Fruit is a dominant food source in the diet of most gibbon species (McConkey *et al.* 2002; Fan *et al.* 2009; Fan *et al.* 2013; Ni *et al.* 2014), likely due to the fact that fruits contain more readily available energy than other plant tissues (Barton & Whiten 1994; Rothman *et al.* 2006; Felton *et al.* 2009c). However, they cannot rely entirely on fruit alone (Chivers 1998), as fruit contains insufficient protein (Rothman *et al.* 2006; Rothman *et al.* 2011; Behie & Pavelka 2012a), which is necessary for survival and reproductive success (Mattson 1980; Felton *et al.* 2009a; Grandison *et al.* 2009). This suggests that young leaves are being added to the diet here to meet protein requirements. This is important for captive animals where it should be ensured that protein sources are added to a fruit based diet.

Dietary fibres are composed of hemicellulose, cellulose, and lignin and are not easily digested by primates with simple stomachs such as gibbons (Cork & Foley 1991; Rothman *et al.* 2006), and consequently fibre is generally considered negative nutrients (Van Soest 1978; Shah *et al.* 1982). In order to digest fibres, animals must depend on gut micro-organisms to utilize dietary fibres for the production of fatty acids and microbial protein (Cork & Foley 1991; Clements *et al.* 2009). Although most studies find that mature leaves consumed by primates have higher fibre contents than other plant tissues (Oates *et al.* 1980; Felton *et al.* 2009c; Behie & Pavelka 2012a), this study found that the mature leaves from three plant species, two epiphytes (*D. ruscifolia* and *Dischidia. sp*) and an liana (Vor Chrey Sleptom), had similar amount of fibre to other plant tissues. In addition, the amount of fibre in all food items was similar. This unusual result may be due to *N. annamensis* in this group consuming the entire fruit of some species including both seeds and their skins, especially *G. macrostachyum*, which are more fibrous than the pulp, bulking up the fibre content of the fruit samples.

Although about 30% of food consumed by *N. annamensis* contained condensed tannins, most primates avoid food with high concentration of such secondary compounds (Glander 1982; Barton & Whiten 1994). Plants that contain high concentrations of condensed tannins are typically difficult to digest, lack nutritional value, and may contain toxins (Milton 1979; Oates *et al.* 1980; Acamovic & Brooker 2005). However, condensed tannins provide nutritional benefits as they bind proteins and polysaccharides (Carrai *et al.* 2003), but also can negatively affect the digestibility of these molecules (Glander 1982; Kool 1992). The flowers (43%) consumed by *N. annamensis* in the present study contained more often condensed tannins than other plant tissues. These flowers were high in fibre, but also

contained protein, which may have provided benefits greater than the costs of the tannins. Although not tested here, flowers may also be a source of minerals for the gibbons as they have been found to contribute relatively high levels of calcium and phosphorous to diets of chimpanzees (Hladik 1977).

3.4.2 Balance of nutrients in foods eaten by *Nomascus annamensis*

The RMT (Figure 3.9) shows that this group of gibbons predominantly consumed food items with a high concentrations of TNC. However, these individuals also consumed other plant tissues to gain protein and lipids. This contradicts other studies, where protein-rich foods are the main target for primates (Milton 1979; Rothman *et al.* 2006; Felton *et al.* 2009a). This prioritization of protein in the diet can be seen at a daily level, with some primate species maintaining a daily intake of protein while allowing carbohydrate and lipid intake to fluctuate (Felton *et al.* 2009b; Johnson *et al.* 2013). However, this study indicates that this group of *N. annamensis* consumed more food with a high concentration of TNC, while only a few food items were higher in protein, and lipids was lower in all plant tissues.

Flowering, and the availability of fruit and young leaves, changes seasonally in Southeast Asian tropical forests (Hamilton & Galdikas 1994; Wendeln *et al.* 2000; McConkey *et al.* 2002; Hanya & Bernard 2012), and some gibbon species shift their diet from fruit to young leaves according to season and the availability of food sources (McConkey *et al.* 2002; Fan *et al.* 2009; Fan *et al.* 2013). Although gibbons are considered fruit specialists, black crested gibbons (*Nomascus concolor*) consume more young leaves than fruit in harsh environments (Ganasia *et al.* 2008; Fan *et al.* 2009). Likewise, fruit forms a considerable part of gorillas (*Gorilla. spp*) diets (Doran-Sheehy *et al.* 2009). However, the mountain gorillas (*G. beringei*) consume more young leaves to increase protein intake, possibly to compensate for carbohydrate-rich fruit (Rothman *et al.* 2011). The present study found *N. annamensis* eat a diet high in carbohydrate-rich fruit, but they may later switch to consume more young leaves or insects to meet protein requirements at different times of year (Frechette *et al.* in prep).

The RMT model also shows that some key food species play very important roles in providing good sources of both TNC and protein for *N. annamensis*. Fruit from the tree *M. elliptica* and the liana *W. edulis* (Appendix 2, Figure 8) were the two richest sources of TNC, while young leaves from two tree species *M. duperreana* (Appendix 2, Figure 8) and *L. elegans* were among the few species providing a rich source of protein (Figure 3.9).

Although most plant species contained low proportions of lipids, some species were the main sources of lipids, including young leaves of tree *G. oliveri* and liana Vor Krovanh. Figs (*Ficus. sp*) were also one of the most important plant species for *N. annamensis* due to their high carbohydrate levels, though their comparatively low levels of protein and lipids may necessitate the consumption of other types of fruit and young leaves. Figs are an important, nutritionally balanced food source for spider monkeys (*Ateles chamek*) due to their available lipids and proteins (Felton *et al.* 2009b). The fruit of some species may have a high concentration of required nutrients, while others have low concentrations, or have evolved secondary compounds to avoid consumption by herbivores (Ryan 1989; Speiser & Rowell-Rahier 1991). Consequently, not all plant species available are consumed by animals; for example, the black crested gibbon (*Nomascus concolor*) selects only 77 plant species as food sources from their entire territory, and spend the majority of time feeding on only 10 plant species (Fan *et al.* 2009), similarly to that was found here (Chapter 2). This study clearly indicates that plant species selected by the study group of *N. annamensis* play varying and important nutritional roles to maintain the population of this study group.

The nutritional chemistry of plant tissues is spatially and temporally variable (Rothman *et al.* 2006). Several factors are expected to influence the nutritional compositions of each plant tissue, including the maturity of the plant tissues, weather, season, temperature, soil type, and exposure to sunlight (Baranga 1983; Chapman *et al.* 2003; Rothman *et al.* 2006). Plant samples were collected for this study in the dry season. As a result, a future study is needed on the nutritional composition of plant tissues consumed by this group in the rainy season. The results show all plant tissues had different nutritional values, with fruit a good source for TNC, while young and mature leaves were a good source of protein and moisture, respectively. To balance nutritional requirements, the group of *N. annamensis* needs to consume varieties of plant tissues from different plant species. Consequently, some plant species that this group of gibbons selected for food play very important roles in maintaining the nutrient intake required by this species, and they need special protection for the long-term conservation for *N. annamensis*.

3.5 Summary

The present study demonstrates that all plant tissues consumed by *N. annamensis* had different nutritional values, suggesting animals are nutrient balancing. Mature leaves had the highest moisture content, while young leaves had significantly high values of protein, and fruit contained high levels of TNC. All food items consumed by this group of gibbons had similar amounts of fibre (NDF, ADF, and ADL), whereas flowers had a higher frequency of condensed tannins than other consumed plant tissues. Generally, food items selected by this gibbon species were high in TNC, with only a few high in protein, and all items had low levels of lipids.

The results from this research contribute to long-term conservation programs for this gibbon species. When developing feeding plans for this species in captivity, fruit and young leaves should be included, with an emphasis on fruit-rich carbohydrates. Key plant species selected by this group of gibbons, in particular *I. umbellulata*, *Ficus. sp*, *L. elegans*, *G. oliveri* and *W. edulis*, must be protected as they provide good nutritional input, and appear to be the main plant species that this group of gibbons rely on in their small territory in the dry season.

Considering this study was conducted in the dry season, food selection by this group in the rainy season should be considered in order to compare food types selected throughout the year, and to show if their nutritional requirements vary between seasons. Insects are good sources of protein in other gibbon species, and great apes like mountain gorillas (Chivers 1998; Borah *et al.* 2014; Rothman *et al.* 2014), and considering *N. annamensis* were observed to occasionally eat insects in the present study, future studies on insects selected by this species are needed to elucidate what nutritional value these insects provide.

Chapter 4

General conclusions and implications for conservation

4.1 Summary of research findings

Optimal foraging theory states that animals should balance energy output and intake so that energy intake is maximised in relation to the costs of finding and ingesting food (MacArthur & Pianka 1966; Cowles *et al.* 1988; Belovsky 1997). Animals, including primates, must make a choice about what types of food items to include in their diets, as different foods can affect lifespan, health, social relationships, fitness and reproduction and have various costs associated with them (Fernandes *et al.* 1976; Koenig *et al.* 1997; Givens & Shingfield 2004; Felton *et al.* 2009a; Grandison *et al.* 2009; Harris *et al.* 2010; Trepanowski *et al.* 2011). Tropical plants provide a wide range of potential food sources, but not all plant species and tissues are selected by animals (Westoby 1974; Oates *et al.* 1980). Some plant species have evolved both physical and chemical defences, and as a result some animals avoid consuming these plant species (Wittstock *et al.* 2004; Rosenthal & Berenbaum 2012).

Gibbons are the smallest apes in the world (Mootnick & Fan 2011; Carbone *et al.* 2014), and populations have declined significantly worldwide due to habitat destruction and hunting pressure (Cheyne *et al.* 2008). Gibbons are usually frugivores (Lappan & Whittaker 2009), but their diet is supplemented by young leaves, flowers, mature leaves, and insects (McConkey *et al.* 2002; Fan *et al.* 2009; Fan *et al.* 2013). Most gibbons are listed as Critically Endangered and Endangered by IUCN Red List, and several species are likely to go extinct without conservation effort (Gray *et al.* 2010). The northern yellow-cheeked crested gibbon (*Nomascus annamensis*) is a recently described species (Thinh *et al.* 2010), and less is known about this species than other gibbons. To assist the development of a long-term conservation program for this gibbon species, this study addressed five research questions. The findings of these are summarised below.

Overall, the members of the study group of *N. annamensis* spent the majority of their time resting, followed by feeding, travelling and socializing. All group members (adult male, adult female, sub-adult male and juvenile male) spent similar amounts of time in each of these activity categories. This shows that social animals like this group of *N. annamensis* may have similar activity budgets.

The study group of *N. annamensis* selected 37 plant species for their food sources, although only 16 of these were consumed for the majority of time. The relative density of these plant species was very low inside the home range of this group, with the 10 most selected plant species representing less than 7% of the total density of tree and liana species in the area. This indicates that *N. annamensis* specifically selects comparatively rare species as food over more common plant species, suggesting that something other than availability is dictating their choices.

Like other gibbons, fruit was the main food for this group, supplemented by young leaves, flowers, mature leaves, and occasionally insects. The gibbons in this group spent more time feeding on flowers when they became available, however, there was no relationship between the availability of fruit or young leaves and the amount of time *N. annamensis* individuals spent feeding on them, suggesting flowers may be a preferred food item at this time of year. The lack of relationship between the availability of fruit and feeding time may be because densities of plant species selected by *N. annamensis* were very low inside the home range of this animal, although some plants produced a large quantity of fruit. In addition, young leaves may be used mainly as an alternative food source, where a preferred item is low in abundance. The study group of *N. annamensis* were not observed feeding on mature leaves from the top 10 plant species.

Mature leaves had the highest concentration of moisture, followed by young leaves and flowers, while fruit had the lowest, and this may be because the fruits selected by northern yellow-cheeked crested gibbons were less pulpy and tougher than the fruits other gibbons may choose (McConkey *et al.* 2002). Young leaves contained more than double the protein of flowers, fruit and mature leaves, suggesting they are eaten to meet the protein demands of this group. Most plant tissues had a low level of lipids, but fruit contained more lipids than other plant tissues, due to the seeds that were ingested with some fruit species. The level of total non-structural carbohydrate (TNC) was highest in fruit, likely due to the high sugar content. All plant tissues had similar fibre contents including, NDF, ADF and ADL. While this is an unusual result, it may be due to the ingestion of seeds and tough skin with fruits that increased their fibre content to a similar level to that of leaves. About one third of all plant tissues consumed by *N. annamensis* contained some condensed tannins, and flowers had the higher frequency of condensed tannins. All these findings clearly demonstrate that plant tissues selected by this group of *N. annamensis* had different nutritional values. The gibbons fed on fruit for TNC and lipids, while young leaves were consumed for protein,

mature leaves for moisture, and flowers provided TNC and other nutrients, although they contained more condensed tannins than other plant tissues.

The right-angle mixture triangle (RMT) model indicated that this group of gibbons consumed food items with more TNC than protein, and most food items were low in lipids. This reflects the fact that this group of *N. annamensis* spent more time feeding on fruit than other plant tissues, and those fruits were rich in TNC. This model also showed that plant species selected by this group of *N. annamensis* provided different nutritional benefits. Some plant species provided a majority of fruit resources that were high in TNC, and some plants provided a majority of young leaves that were good sources of protein, while others provided both flowers and young leaves that were good sources of both TNC and protein. All plant tissues selected by *N. annamensis* were low in lipids.

4.2 General discussion

The study of the behavioural ecology of animals helps conservationists predict factors that may influence their behaviours (Sutherland 1998). This is important because some behaviours may negatively impact survival rates (Siemers & Schaub 2011; Hardus *et al.* 2012). The present study showed that the study group of *N. annamensis* spent most of the time resting, and the remaining time feeding, travelling, and socializing, in that order. In normal conditions, hoolock gibbons (*Hoolock hoolock*) spend more time feeding than other activities (Islam & Feeroz 1992). However, in cold habitats (an average temperature of < 10 °C), eastern hoolock gibbons (*Hoolock leuconedys*) spend more time resting than other behaviours, which indicates that gibbons may need to conserve energy when at high latitudes and in cold habitats (Fan *et al.* 2013). This may also be affected by rainfall, which requires additional thermoregulation (Watanuki & Nakayama 1993; Fan *et al.* 2013). While February has one of the coldest minimum temperatures in Cambodia, the minimum temperature at the study site during the dry season (November to April) was 15.5 °C (Nelson 2014), which is not dramatically different to the wet season. There was also no rainfall during the study period. This indicates that thermoregulatory factors are unlikely to have influenced the behaviour of this gibbon group over the course of this study.

Noise can alter animal behaviours (Brumm 2004; Lengagne 2008). Noise can affect mate attraction, reproductive success (Halfwerk *et al.* 2011) and territory defence (Slabbekoorn & Ripmeester 2008). Noise associated with logging can impact the behaviour and activity budgets of primate species (Pontes & Soares 2005; Hardus *et al.* 2012), and in this study inactive activity increased in March when chainsaw use was at its highest in the study areas (pers. observation), indicating that chainsaws may be impacting energy and activity budgets in this group. This finding, however, is preliminary, and future studies are needed to determine whether resting is the normal dominant behaviour for this group of gibbons, or if there are any other factors that influence these behaviours, such as anthropogenic noise pollution and selective logging.

Food sources that are reliable and of sufficient quantity and quality are hugely important for all organisms on the planet (Leibold & Wilbur 1992; Mead *et al.* 1999; Grandison *et al.* 2009). As a result, to have successful long-term conservation programs and captive breeding programs, it is important to know which types of foods and what nutritional

compositions are selected by animals in the wild to maintain survival and reproduction (Kleiman *et al.* 1986). Most gibbon populations have declined considerably due to habitat destruction and hunting (Geissmann 2007; Cheyne *et al.* 2008; Gray *et al.* 2010). Little is known about the feeding ecology of gibbons in general, and even less is known about crested gibbons, which leads to difficulty in conservation. Based on the results from this study, captive *N. annamensis* should be provided not only with fruit, but also with young leaves, and priority should be given to the 16 species consumed most often by the group in this study (Table 2.3), although additional research is needed to see what food species are eaten by other groups of *N. annamensis*.

It is vital to protect habitat and food plants for the long-term conservation of most primate species (Medley 1993; Gates 1996). Gibbons live in small groups (Fan *et al.* 2010), with small territories (Chivers & MacKinnon 1977). They completely rely on resources available in their relatively restricted home range for survival (Marshall & Marshall 1976). Moreover, not all plant species in their territory are edible, or appropriate food sources (Fan *et al.* 2009; Fan *et al.* 2013). Any logging which damages feeding plants would negatively impact both the lifespan and reproductive success of *N. annamensis*, as with other primate species (Plumptre & Reynolds 1994; Chapman *et al.* 2000; Thompson & Wrangham 2008; Mattison *et al.* 2012), and should be avoided. *N. mutabile* and Neang Kmov were the most common tree species inside the home range of this group of *N. annamensis*. *N. mutabile* bear fruit in late April that are consumed by white-handed gibbons (*H. lar*) in Thailand (Whiten *et al.* 1991) and both *N. mutabile* and Neang Kmov were also confirmed by local guides as gibbon feeding on plant species. However, during the study period, the study group of *N. annamensis* were not observed feeding any plant tissues from those plant species. Furthermore, the relative density of the 10 most selected plant species in the home range of the study group was very low, indicating their disproportionate importance for *N. annamensis*. For example, the relative density of *Ficus. sp.*, which was one of the most important food species, was just 0.41%, but it bore fruit from January until early April providing a constant fruit source in these months. These data clearly indicate that the gibbons selected rare over common plant species, and this suggests that protection of these food species is even more crucial. Moreover, if logging reduces the abundance of feeding plant species, this group of *N. annamensis* will need to travel long distances to find appropriate food sources during the dry season.

The majority of plant species selected by *N. annamensis* were high in TNC, with some species high in protein, but all plant tissues were low in lipids. For instance, the tree *M. elliptica* and the liana *W. edulis*, which were the top two food plant species, provided good sources of TNC, while the tree *M. duperreana*, another important food species, provided a good source of protein. Consequently, plant species selected by this group of gibbons have significantly different yet equally necessary nutritional values, and special protection and increasing density of those plant species would contribute positively to long-term conservation for this gibbon species.

Five main models have been proposed for primate nutritional goals, including (i) maximising protein, (ii) maximizing energy, (iii) limiting fibre content, (iv) avoiding secondary compounds, and (v) balancing nutritional values (Schoener 1971; Freeland & Janzen 1974; Milton 1979; Mattson 1980; Raubenheimer & Simpson 2004; Felton *et al.* 2009a). This study found that food items consumed by *N. annamensis* had high concentrations of TNC, while only a few items were high in protein. This contradicts a study in similarly frugivorous spider monkeys (*Ateles chamek*) that prioritized protein in their daily intake, and allowed carbohydrate and lipids intake to fluctuate (Felton *et al.* 2009b). Similarly, mountain gorillas (*Gorilla beringei*) consumed more food (young leaves) with high concentrations of protein when they became available (Rothman *et al.* 2011). Other studies indicate gibbons gain more protein content from insects rather than plant tissues (Chivers 1998; Borah *et al.* 2014; Ni *et al.* 2014). As the present study did not measure the amount of food ingested daily, there is no evidence at present to reject or support whether that *N. annamensis* prioritizes protein and allows levels of other nutrients to fluctuate. However, the results from the present study do shed light on the diet of this species. *N. annamensis* consumed more food items with high concentrations of TNC, and few foods chosen were high in protein. This prioritisation of TNC makes sense, considering the fact that TNC is commonly found in fleshy fruit, and is a good source for energy (Barton & Whiten 1994). A long-term study on food selection by *N. annamensis* as well as a specific study on the nutritional value of insects consumed by this species should be undertaken to further elucidate the feeding habits of this species.

The studied group of *N. annamensis* spent most of the time feeding on fruit, which provide good sources for carbohydrate that contribute more than 40% of the metabolizable energy in primates' diets (NRC 2003). In addition, they also spent time feeding on young leaves, which are also good sources for protein. These information indicate that this group of

N. annamensis selected high quality food sources over lower quality food items, and of the five nutritional models described above, this food selection may best support the energy maximization theory (Schoener 1971).

Plant cell walls generally cannot be broken down by animals with simple stomachs (Milton 1999), and this may explain why some primates select food items with low concentrations of fibre (Davies *et al.* 1988; Barton & Whiten 1994; Hanya & Bernard 2015). The results of the present study indicate that similar levels of all fibres (NDF, ADF, and ADL) were found in the different plant tissues consumed by this group of gibbons. As a consequence, the current results suggest that *N. annamensis* does not limit its fibre intake. This result differed from other studies in that fruit generally contains lower fibre content than leaves (Oates *et al.* 1980; Felton *et al.* 2009c; Behie & Pavelka 2012a). This may be due to the fact that the ingestion of seeds and tough skin with fruits increased their fibre concentration. However, future studies on the nutritional composition of unselected food items should be conducted in order to understand whether those non-food plants have higher concentrations of fibre than selected foods.

Some plants have evolved a wide range of secondary metabolites to avoid consumption by herbivores (Wittstock *et al.* 2004; Rosenthal & Berenbaum 2012). Plants containing secondary compounds are often bitter and even toxic (Acamovic & Brooker 2005), so most primates avoid food items with high concentrations of these compounds (Glander 1982; Barton & Whiten 1994). This study measured only one type of secondary compound, condensed tannins, in each plant sample, and the result indicates that more than 30% of plant tissues consumed by *N. annamensis* contained condensed tannins, particularly flowers. Condensed tannins consumed by animals may have both negative and positive effects (Rothman *et al.* 2006). Food items containing this compound may have reduced nutritional quality, decreased digestibility, and reduced palatability (Reed 1995), but tannins also contribute to protection from intestinal parasites, pathogenic bacteria and fungi (Chung *et al.* 1998; Min & Hart 2003). Primates may even deliberately consume foods containing condensed tannins for self-medication (Barton & Whiten 1994; Carrai *et al.* 2003). As food items consumed by *N. annamensis* still contained condensed tannins, this study has no evidence that gibbons avoid foods containing these secondary compounds. More studies are needed to link the consumption of secondary compounds to parasite infections, and compare these compounds between food and non-food items.

To ensure continued survival and reproductive success, animals need to balance nutritional intakes from the food that they eat (Whiten *et al.* 1991; Raubenheimer & Simpson 1997). Although some primate species prefer young leaves (Barton & Whiten 1994; Carrai *et al.* 2003), which have high levels of protein (Felton *et al.* 2009c; Rothman *et al.* 2011; Hanya & Bernard 2015), they may need to consume fruit, seeds or insects to balance their nutritional requirements (Whiten *et al.* 1991; Borah *et al.* 2014; Rothman *et al.* 2014; Hanya & Bernard 2015). The present study demonstrates that *N. annamensis* individuals did not change the time they spent feeding food items depending on either their availability or their nutritional composition. The group of *N. annamensis* spent more time feeding on flowers when they became available. This may be because flowers contained significant levels of nutrients and minerals (Rop *et al.* 2012) that are required by *N. annamensis*.

The knowledge from this thesis may help a long-term conservation of *N. annamensis*. This study suggests that key food plant species, *I. umbellulata*, *Ficus. sp*, *L. elegans*, *G. oliveri*, *W. edulis*, and *M. elliptica* should receive additional protection. Total non-structural carbohydrates are generally gained from fresh fruit, and they are an important dietary component for this species of gibbon. Young leaves provide good sources for protein. Therefore this thesis has assisted both wild and captive conservation programs for northern yellow-cheeked crested gibbons as well as augmenting behavioural ecological knowledge for this recently discovered species.

4.3 Implications for conservation

Although the northern yellow-cheeked crested gibbon (*N. annamensis*) has not yet been listed in the IUCN Red List, it is likely to be listed as Endangered as it faces similar threats to other gibbons (Thinh *et al.* 2010). This species plays a crucial role in seed dispersal (Frechette 2014), which maintains forest structure. Reducing the population of this gibbon species may therefore alter forest ecosystems (Nuñez-Iturri & Howe 2007). Consequently, scientific knowledge is urgently needed for a long-term conservation program of this gibbon species to be successful.

4.3.1 Food plant selection

While most of the plant species selected for food by *N. annamensis* in this study are currently not targeted for commercial timber collection in the VSSPCA, two of the top 10 food species, *D. alatus* and *D. cochinchinensis*, are targeted for logging (pers. comm. from local villagers). The Dipterocarpaceae are both ecologically and commercially valuable (Appanah & Turnbull 1998; Bunyavejchewin *et al.* 2003), and their wood dominates international tropical timber markets (Whitmore & Burnham 1975). The combination of high demand for house construction (Schmidt & Nguyen 2005) and unsustainable timber collection practices have now rendered most dipterocarps under threat (Appanah & Turnbull 1998). Although other plant species selected by *N. annamensis* are not commonly collected for construction, local people collect some species including *G. oliveri*, *M. elliptica* and *W. edulis* for daily consumption (pers. comm. from local villagers). For example, local communities in Ratanakiri province collect stems of *W. edulis* for traditional medicine, and their fruits for sale and household consumption (Laval *et al.* 2011). There is no actual inventory of plant species in the VSSPCA area yet, however, the relative densities of those selected plants are very low inside the home range of the study group of *N. annamensis*. This indicates that special protection is needed to ensure that these important food plant species are sufficiently protected to sustain the survival of this group of gibbons.

4.3.2 Illegal logging and hunting pressure in the VSSPCA

In the last decade, the VSSPCA has been protected by the cooperation of the Forestry Administration, the Cambodian government, and the non-profit organization Conservation International. Consequently, although valuable trees have been cut down from other locations, this area still contains relatively large numbers of most commercially logged plant species (pers. observation). Unfortunately, large plants in the VSSPCA are now being targeted for timber collection (pers. comm. from local villagers). Should larger trees decline in number as a result of this logging, there is a risk that smaller trees will then be targeted as they become economically viable (Sasaki 2006), with associated declines in habitat quality and food availability for *N. annamensis*. During the study period, illegal logging was occasionally observed inside the home range of the study group, and frequency was observed around VSSPCA. While these logged trees were not gibbon food plant species, these activities may negatively impact the behaviour of *N. annamensis*. In addition, previous work has found that *N. annamensis* rely on large and tall trees for calling and sleeping, and if logging target those tree species, the gibbon group may suffer (Nelson 2014). Other studies indicate that some gibbons are being targeted for poaching (Geissmann 2007; Phoonjampa & Brockelman 2008; Malone *et al.* 2014), although gibbons at the VSSPCA have a low rate of hunting, and just recently the hunting of a gibbon has been confirmed (pers. comm. from villagers). In addition, local people hunt other primates and animals for food and traditional medicines (Hill 2011). Lorises are the most common hunted primates for traditional medicine (Pollard *et al.* 2007; Starr *et al.* 2010; Hill 2011), while gibbons are likely live-caught and kept as pets (Johnson *et al.* 2005; Pollard *et al.* 2007). Considerably, hunting may not the main threat to gibbons at the study site; instead, illegal logging and deforestation are of considerable concern for the conservation of this species and its habitat.

4.3.3 Possibility of captive breeding

Captive breeding of animals has become a popular method for conservation, particularly for endangered species (Philippart 1995; McPhee 2004). After being bred in zoos, animals are trained to find food, then released or reintroduced into their natural habitats (Beck *et al.* 1994). This method has prevented the extinction of some species (Ebenhard 1995; Fraser 2008). The endangered white-handed gibbon (*H. lar*) became locally extinct in Phuket Island, Thailand, but eight families (30 individuals) have been introduced to the island

(Osterberg *et al.* 2014). After 10 years, over half of the reintroduced populations have survived (Osterberg *et al.* 2015).

Captive breeding, when combined with reintroductions, is an important tool for conserving threatened populations. However, in order to maintain successful captive breeding programs, the correct food must be provided to captive individuals. Ascertaining the correct type, amount, and nutritional composition of food is a priority, especially for species that have never been captive before. Currently, knowledge of ideal food and nutritional regimes for captive gibbons is limited, and even more so for crested gibbons (NRC 2003). During the study period, a baby *N. annamensis* was rescued (Appendix 3, Figure 1) and sent to the Phnom Tamao Wildlife Recuse Centre (Appendix 3, Figure 2). This incident provides further motivation to develop a feeding regime for this species from observations gathered over the course of the current study. If there are any chances for captive breeding of *N. annamensis*, this study suggests that food items provided to this species should include a majority of fruit, supplemented with young leaves from *M. duperreana*, *L. elegans*, and Vor Krovanh. Although this study would suggest insects are also another alternative food items for this gibbon species, future study is needed to clarify which insect species are targeted and what nutritional values they contain.

4.4 Conclusions

Individuals in the study group of *N. annamensis* (group A) each spent similar amounts of time on each activity. All group members spent most of the time resting, with the remainder of the activity budget spent on feeding, travelling, and socializing, in that order. *N. annamensis* individuals observed in the present study selected almost 40 trees and lianas for their food sources, but predominately fed on only 16 species. The relative density of most of these preferentially selected species was very low, although some of those plants produced a large quantity of fruit, and as *N. annamensis* is predominately frugivorous, such fruit-bearing plants could be expected to contribute significantly to its sources of food.

Fruit was the main diet for this gibbon species, with alternative food items including young leaves, flowers, mature leaves, and insects. The gibbons spent more time feeding on flowers when they became available, indicating a switch in diet and an active preference for flowers. However, no relationships were found between feeding times and the availability of fruit or young leaves. Fruit consumed by *N. annamensis* had high concentrations of TNC and lipids, while young leaves had high level of protein, and mature leaves had a high water content. Condensed tannins were more present in flowers consumed by this gibbon species than in fruit, mature leaves or young leaves. All plant tissues had similar amount of fibre (NDF, ADF, and ADL). A RMT reveals that most food items selected by this group of gibbons had high levels of TNC, while a few plant species had high concentrations of protein, and all food items were low in lipids.

The findings of this thesis contribute to long-term conservation programs for northern yellow-cheeked crested gibbons (*N. annamensis*) both in the wild and captivity. The key plant species selected by the study group of *N. annamensis*, in particularly *I. umbellulata*, *Ficus. sp*, *L. elegans*, *G. oliveri*, *M. duperreana* and *W. edulis*, should have additional protection. Selective logging of food plant species should be avoided because reduced food availability is likely to affect the population size of primates (Plumptre & Reynolds 1994; Chapman *et al.* 2000; Thompson & Wrangham 2008; Duarte *et al.* 2011). Introduction programs for *N. annamensis* should ensure that these plant species grow in the rehabilitation site. Knowledge of food items that should be provided for captive breeding for *N. annamensis* is sparse, however, this study suggests that food should include fruit and young leaves because fruit provide good sources for TNC, and young leaves provide protein.

4.5 Limitations

Safety is the main concern when collecting data at the field, so experienced local assistants were needed for this study. Daily data collection was impractical and therefore focal observations were performed two to five days per week. Also, on occasion, the gibbon group could not be found. The level of plant diversity in VSSPCA is very high and it was difficult to identify all species. In some cases even local names for some species were not known and these were labelled as unknown.

It would have been preferable for the phenological data to be collected inside the 20 vegetation plots, not along the transect lines as the trees and lianas inside the 20 vegetation plots are more evenly distributed than the trees and lianas along the transect lines. However, time constraints at the beginning of the data collection period meant that phenological data was collected from the transect lines, which had been set up inside the home range of the gibbon study group by the team from Forestry Administration and Conservation International.

Not all food items that this group of gibbons consumed were collected for nutritional analysis. This was due to the difficulty of collecting plant samples from large and tall trees. Moreover, other trees produced a small amount of young leaves or flowers, and there were not enough remaining for sample collection. The study period was only three months (January to early April 2015), so I cannot generalize that plant species selected by this group of gibbons are the only important feeding plant species year-round. Ideally, the study should continue for at least one year, but this is clearly beyond the scope of this thesis.

4.6 Future directions

This thesis investigated food selection by a group of *N. annamensis* in northern Cambodia, and the aim of this thesis was to contribute to a long-term conservation program for this particular species. Throughout the course of this research, new interesting research questions have been suggested. The answers to these questions will be important for the long-term conservation for this gibbon species and will extend the findings of this study.

It is likely that logging inside the home range of this group of gibbons may influence the behavioural ecology of this species, as it does for other primates (Pontes & Soares 2005; Hardus *et al.* 2012). Future studies should examine the impact of illegal logging and how it overlaps with food plants as well as determining whether noise pollution from chainsaws influences activity budgets of *N. annamensis*. More importantly, this group of gibbons has been habituated to humans, with the main goal of attracting tourists to visit the site. Increased numbers of tourists influence animal ecological behaviours, leading to stress (Wells 2005; Behie *et al.* 2010), and may expose them to human diseases (Woodford *et al.* 2002; Malone *et al.* 2010). Future studies should compare the level of stress and contamination of human diseases between a group of gibbons visited by tourists and a non-visited group. Such of the study (the level of stress) is set to commence in 2016 (Behie pers. comm.).

This study indicated that most food items consumed by this gibbon species were high in TNC, so it did not show that primates maximize protein intake as for other primates (Felton *et al.* 2009b; Johnson *et al.* 2013). However, since some gibbons and other apes may gain protein by consuming insects rather plant tissues (Chivers 1998; Borah *et al.* 2014; Rothman *et al.* 2014), future studies should consider collecting and identifying insects consumed by this gibbon species for nutritional analyses. The results from this type of study would improve our understanding of the food requirements for this gibbon species in captive breeding.

Due to limited time of the research, this study was conducted only on one group of gibbons, and compared diet selection only between group members, and was only conducted in the dry season. However, food and nutritional selection by primates may be different among groups, age, and sex classes (Rothman *et al.* 2008b). Future studies should compare food selection in a larger sample of groups over a whole year to see how these current results compare.

To give a good recommendation for gibbons in captive breeding, knowing food items and their nutritional values may not be enough. Most living organisms including animals and plants require minerals as structural components of organs and tissues (NRC 2003). Future studies should not only collect plants for analysing nutritional compositions, but minerals should be considered.

Bibliography

- Acamovic T. & Brooker J. (2005) Biochemistry of plant secondary metabolites and their effects in animals. *Proceedings of the Nutrition Society* **64**, 403-12.
- ADB (2014) Cambodia: Country poverty analysis 2014, Asian Development Bank (ADB).
- Altmann J. & Alberts S.C. (2005) Growth rates in a wild primate population: Ecological influences and maternal effects. *Behavioral Ecology and Sociobiology* **57**, 490-501.
- Altmann J., Altmann S.A., Hausfater G. & McCuskey S.A. (1977) Life history of yellow baboons: physical development, reproductive parameters, and infant mortality. *Primates* **18**, 315-30.
- Alves R.R.N., Rosa I.L., Albuquerque U.P. & Cunningham A.B. (2013) Medicine from the wild: an overview of the use and trade of animal products in traditional medicines. In: *Animals in Traditional Folk Medicine* (pp. 25-42. Springer.
- Appanah S. & Turnbull J.M. (1998) *A Review of Dipterocarps: Taxonomy, Ecology, and Silviculture*. Centre for International Forestry Research, Bogor, Indonesia
- Avtar R., Sawada H., Takeuchi W. & Singh G. (2012) Characterization of forests and deforestation in Cambodia using ALOS/PALSAR observation. *Geocarto International* **27**, 119-37.
- Baird I.G. & Dearden P. (2003) Biodiversity conservation and resource tenure regimes: a case study from northeast Cambodia. *Environmental Management* **32**, 541-50.
- Baranga D. (1983) Changes in chemical composition of food parts in the diet of colobus monkeys. *Ecology*, 668-73.
- Barney K. (2005) *Customs, Concessionaires and Conflict: Tracking Cambodia's Forest Commodity Chains and Export Links to China*.
- Barton R.A. & Whiten A. (1994) Reducing complex diets to simple rules: food selection by olive baboons. *Behavioral Ecology and Sociobiology* **35**, 283-93.
- Beck B.B., Rapaport L.G., Price M.S. & Wilson A.C. (1994) Reintroduction of captive-born animals. In: *Creative conservation* (pp. 265-86. Springer).
- Behie A.M. & Pavelka M.S. (2012a) Food selection in the black howler monkey following habitat disturbance: implications for the importance of mature leaves. *Journal of Tropical Ecology* **28**, 153-60.
- Behie A.M. & Pavelka M.S. (2012b) The role of minerals in food selection in a black howler monkey (*Alouatta pigra*) population in Belize following a major hurricane. *American Journal of Primatology* **74**, 1054-63.

- Behie A.M., Pavelka M.S. & Chapman C.A. (2010) Sources of variation in fecal cortisol levels in howler monkeys in Belize. *American Journal of Primatology* **72**, 600-06.
- Belovsky G.E. (1984) Herbivore optimal foraging: a comparative test of three models. *American Naturalist*, 97-115.
- Belovsky G.E. (1997) Optimal foraging and community structure: the allometry of herbivore food selection and competition. *Evolutionary Ecology* **11**, 641-72.
- Bender D.J., Contreras T.A. & Fahrig L. (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* **79**, 517-33.
- Biere A., Marak H.B. & van Damme J.M. (2004) Plant chemical defense against herbivores and pathogens: generalized defense or trade-offs? *Oecologia* **140**, 430-41.
- BirdLifeInternational (2015) Species factsheet: *Thaumatibis gigantea*. *BirdLife International*.
- Boesch C., Bi Z.B.G., Anderson D. & Stahl D. (2006) Food choice in Tai chimpanzees: are cultural differences present? *Cambridge Studies in Biological and Evolutionary Anthropology* **48**, 183.
- Boonratana R., Das J., Yongcheng L., Htun S. & Timmins R. (2008) Mocoa leonina. The IUCN Red List of Threatened Species. Version 2015. 2.
- Borah M., Devi A. & Kumar A. (2014) Feeding on non-plant food items by Western hoolock gibbon (*Hoolock hoolock*). *Current Science* **107**, 1657-60.
- Brockelman W., Geissmann T., Timmins T. & Traeholt C. (2008) Hylobates pileatus. The IUCN Red List of Threatened Species. Version 2015.2.
- Brook B.W., Sodhi N.S. & Ng P.K. (2003) Catastrophic extinctions follow deforestation in Singapore. *Nature* **424**, 420-6.
- Brooks T.M., Mittermeier R.A., Mittermeier C.G., Da Fonseca G.A., Rylands A.B., Konstant W.R., Flick P., Pilgrim J., Oldfield S. & Magin G. (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* **16**, 909-23.
- Brumm H. (2004) The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology* **73**, 434-40.
- Buckley C., Nekaris K. & Husson S.J. (2006) Survey of Hylobates agilis albibarbis in a logged peat-swamp forest: Sabangau catchment, Central Kalimantan. *Primates* **47**, 327-35.
- Bunyavejchewin S., LaFrankie J.V., Baker P.J., Kanzaki M., Ashton P.S. & Yamakura T. (2003) Spatial distribution patterns of the dominant canopy dipterocarp species in a seasonal dry evergreen forest in western Thailand. *Forest Ecology and Management* **175**, 87-101.

- Carbone L., Harris R.A., Gnerre S., Veeramah K.R., Lorente-Galdos B., Huddleston J., Meyer T.J., Herrero J., Roos C. & Aken B. (2014) Gibbon genome and the fast karyotype evolution of small apes. *Nature* **513**, 195-201.
- Carrai V., Borgognini-Tarli S.M., Huffman M.A. & Bardi M. (2003) Increase in tannin consumption by sifaka (*Propithecus verreauxi verreauxi*) females during the birth season: a case for self-medication in prosimians? *Primates* **44**, 61-6.
- Ceballos G. & Ehrlich P.R. (2002) Mammal population losses and the extinction crisis. *Science* **296**, 904-7.
- Ceballos G., Ehrlich P.R., Soberón J., Salazar I. & Fay J.P. (2005) Global mammal conservation: what must we manage? *Science* **309**, 603-7.
- Chapman C.A. (1989) Primate seed dispersal: the fate of dispersed seeds. *Biotropica*, 148-54.
- Chapman C.A., Balcomb S.R., Gillespie T.R., Skorupa J.P. & Struhsaker T.T. (2000) Long-Term Effects of Logging on African Primate Communities: a 28-Year Comparison From Kibale National Park, Uganda. *Conservation Biology* **14**, 207-17.
- Chapman C.A. & Chapman L.J. (2002) Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **133**, 861-75.
- Chapman C.A., Chapman L.J., Rode K.D., Hauck E.M. & McDowell L.R. (2003) Variation in the nutritional value of primate foods: among trees, time periods, and areas. *International Journal of Primatology* **24**, 317-33.
- Chapman C.A. & Onderdonk D.A. (1998) Forests without primates: primate/plant codependency. *American Journal of Primatology* **45**, 127-41.
- Chapman C.A., Wasserman M.D., Gillespie T.R., Speirs M.L., Lawes M.J., Saj T.L. & Ziegler T.E. (2006) Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? *American Journal of Physical Anthropology* **131**, 525-34.
- Chatterjee H.J. (2009) Evolutionary relationships among the gibbons: a biogeographic perspective. In: *The Gibbons* (pp. 13-36. Springer.
- Chetry D., Chetry R., Das A., Loma C. & Panor J. (2008) New distribution records for Hoolock leuconedys in India. *Primate Conservation* **23**, 125-8.
- Cheyne S.M., Thompson C.J., Phillips A.C., Hill R.M. & Limin S.H. (2008) Density and population estimate of gibbons (*Hylobates albibarbis*) in the Sabangau catchment, Central Kalimantan, Indonesia. *Primates* **49**, 50-6.
- Chivers D.J. (1998) Measuring food intake in wild animals: primates. *Proceedings of the Nutrition Society* **57**, 321-32.

- Chivers D.J. & MacKinnon J. (1977) On the behaviour of siamang after playback of their calls. *Primates* **18**, 943-8.
- Chung K.-T., Wong T.Y., Wei C.-I., Huang Y.-W. & Lin Y. (1998) Tannins and human health: a review. *Critical reviews in food science and nutrition* **38**, 421-64.
- Clements K.D., Raubenheimer D. & Choat J.H. (2009) Nutritional ecology of marine herbivorous fishes: ten years on. *Functional Ecology* **23**, 79-92.
- Clements T., Gilbert M., Rainey H.J., Cuthbert R., Eames J.C., Bunnat P., Teak S., Chansocheat S. & Setha T. (2013a) Vultures in Cambodia: population, threats and conservation. *Bird Conservation International* **23**, 7-24.
- Clements T., John A., Nielsen K., An D., Tan S. & Milner-Gulland E. (2010) Payments for biodiversity conservation in the context of weak institutions: Comparison of three programs from Cambodia. *Ecological Economics* **69**, 1283-91.
- Clements T., Rainey H., An D., Rours V., Tan S., Thong S., Sutherland W. & Milner-Gulland E. (2013b) An evaluation of the effectiveness of a direct payment for biodiversity conservation: the bird nest protection program in the Northern Plains of Cambodia. *Biological Conservation* **157**, 50-9.
- Clinebell II R.R., Phillips O.L., Gentry A.H., Stark N. & Zuuring H. (1995) Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity & Conservation* **4**, 56-90.
- Coley P.D. (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* **53**, 209-34.
- Coley P.D. & Barone J. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, 305-35.
- Cork S.J. & Foley W.J. (1991) Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defenses in temperate and tropical forests. *Plant Defenses Against Mammalian Herbivory*, 133-66.
- Coudrat C., Rogers L. & Nekaris K. (2011) Abundance of primates reveals Samkos Wildlife Sanctuary, Cardamom Mountains, Cambodia as a priority area for conservation. *Oryx* **45**, 427-34.
- Cowles T., Olson R. & Chisholm S. (1988) Food selection by copepods: discrimination on the basis of food quality. *Marine Biology* **100**, 41-9.
- Cowlishaw G. & Dunbar R.I. (2000) *Primate conservation biology*. University of Chicago Press.
- Dasilva G.L. (1992) The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *Journal of Animal Ecology*, 79-91.

- Davies A., Bennett E.L. & Waterman P.G. (1988) Food selection by two South-east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biological Journal of the Linnean Society* **34**, 33-56.
- De Lopez T.T. (2002) Natural resource exploitation in Cambodia: an examination of use, appropriation, and exclusion. *The Journal of Environment & Development* **11**, 355-79.
- Demott W.R. (1989) Optimal foraging theory as a predictor of chemically mediated food selection by suspension-feeding copepods. *Limnology and Oceanography* **34**, 140-54.
- Detedcc A. & Courchamp F. (2007) Importance of the Allee effect for reintroductions. *Ecoscience* **14**, 440-51.
- Doran-Sheehy D., Mongo P., Lodwick J. & Conklin-Brittain N. (2009) Male and female western gorilla diet: preferred foods, use of fallback resources, and implications for ape versus old world monkey foraging strategies. *American Journal of Physical Anthropology* **140**, 727-38.
- Duarte M.H., Vecci M.A., Hirsch A. & Young R.J. (2011) Noisy human neighbours affect where urban monkeys live. *Biology Letters* **7**, 840-2.
- Duckworth J., Batters G., Belant J., Bennett E., Brunner J., Burton J., Challender D., Cowling V., Duplaix N. & Harris J. (2012) Why South-East Asia should be the world's priority for averting imminent species extinctions, and a call to join a developing cross-institutional programme to tackle this urgent issue. *SAPI EN. S. Surveys and Perspectives Integrating Environment and Society*.
- Duhan A., Chauhan B. & Punia D. (1992) Nutritional value of some non-conventional plant foods of India. *Plant foods for human nutrition* **42**, 193-200.
- Ebenhard T. (1995) Conservation breeding as a tool for saving animal species from extinction. *Trends in ecology & evolution* **10**, 438-43.
- Elder A.A. (2009) Hylobatid diets revisited: The importance of body mass, fruit availability, and interspecific competition. In: *The Gibbons* (pp. 133-59. Springer).
- Engel J. & Lamprecht J. (1997) Doing what everybody does? A procedure for investigating behavioural synchronization. *Journal of Theoretical Biology* **185**, 255-62.
- Fan P.-F., Ai H.-S., Fei H.-L., Zhang D. & Yuan S.-D. (2013) Seasonal variation of diet and time budget of Eastern hoolock gibbons (*Hoolock leuconedys*) living in a northern montane forest. *Primates* **54**, 137-46.
- Fan P.-F., Fei H.-L., Scott M.B., Zhang W. & Ma C.-Y. (2011) Habitat and food choice of the critically endangered cao vit gibbon (*Nomascus nasutus*) in China: implications for conservation. *Biological Conservation* **144**, 2247-54.
- Fan P.-F., Ni Q.-Y., Sun G.-Z., Huang B. & Jiang X.-L. (2008) Seasonal variations in the activity budget of *Nomascus concolor jingdongensis* at Mt. Wuliang, Central Yunnan,

- China: effects of diet and temperature. *International Journal of Primatology* **29**, 1047-57.
- Fan P., Fei H., Xiang Z., Zhang W., Ma C. & Huang T. (2010) Social structure and group dynamics of the cao vit gibbon (*Nomascus nasutus*) in Bangliang, Jingxi, China. *Folia primatologica* **81**, 245-53.
- Fan P., Ni Q., Sun G., Huang B. & Jiang X. (2009) Gibbons under seasonal stress: the diet of the black crested gibbon (*Nomascus concolor*) on Mt. Wuliang, Central Yunnan, China. *Primates* **50**, 37-44.
- Fan P.F. & Jiang X.L. (2008) Sleeping sites, sleeping trees, and sleep-related behaviors of black crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, Central Yunnan, China. *American Journal of Primatology* **70**, 153-60.
- FAO (2010) *Global Forest Resources Assessment 2010 - main report*. FAO Forestry Paper No. 163. Rome. www.fao.org/docrep/013/i1757e/i1757e00.htm.
- Fargione J., Hill J., Tilman D., Polasky S. & Hawthorne P. (2008) Land clearing and the biofuel carbon debt. *Science* **319**, 1235-8.
- Feeny P. (1976) Plant apparency and chemical defense. In: *Biochemical interaction between plants and insects* (pp. 1-40. Springer.
- Felton A.M., Felton A., Lindenmayer D.B. & Foley W.J. (2009a) Nutritional goals of wild primates. *Functional Ecology* **23**, 70-8.
- Felton A.M., Felton A., Raubenheimer D., Simpson S.J., Foley W.J., Wood J.T., Wallis I.R. & Lindenmayer D.B. (2009b) Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behavioral Ecology*, arp021.
- Felton A.M., Felton A., Wood J.T., Foley W.J., Raubenheimer D., Wallis I.R. & Lindenmayer D.B. (2009c) Nutritional ecology of *Ateles chamek* in lowland Bolivia: how macronutrient balancing influences food choices. *International Journal of Primatology* **30**, 675-96.
- Felton A.M., Felton A., Wood J.T. & Lindenmayer D.B. (2008) Diet and feeding ecology of *Ateles chamek* in a Bolivian semihumid forest: the importance of *Ficus* as a staple food resource. *International Journal of Primatology* **29**, 379-403.
- Fernandes G., Yunis E. & Good R. (1976) Influence of diet on survival of mice. *Proceedings of the National Academy of Sciences* **73**, 1279-83.
- Fraser D.J. (2008) How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications* **1**, 535-86.
- Frechette J. (2014) Construction and experimentally testing the impacts of animal generated dispersal kernels in a northern Cambodia. PhD thesis, University of Florida, USA.

- Frechette J., Behie A., Hon N. & Rawson B. (in prep) Seasonal variation in diet and activity budgets of the northern yellow-cheeked crested gibbon (*Nomascus annamensis*) Cambodia
- Freeland W.J. & Janzen D.H. (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist*, 269-89.
- Galbreath G., Mordacq J. & Weiler F. (2006) Genetically solving a zoological mystery: was the kouprey (*Bos sauveli*) a feral hybrid? *Journal of Zoology* **270**, 561-4.
- Ganasia J., Ortmann S. & Robbins M.M. (2008) Food preferences of wild mountain gorillas. *American Journal of Primatology* **70**, 1-12.
- Garber P.A. (1986) The ecology of seed dispersal in two species of callitrichid primates (*Saguinus mystax* and *Saguinus fuscicollis*). *American Journal of Primatology* **10**, 155-70.
- Garber P.A. (1988) Foraging decisions during nectar feeding by tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichidae, Primates) in Amazonian Peru. *Biotropica*, 100-6.
- Gates J.F. (1996) Habitat alteration, hunting and the conservation of folivorous primates in African forests. *Australian Journal of Ecology* **21**, 1-9.
- Geissler P., Hartmann T. & Neang T. (2012) A new species of the genus *Lygosoma* Hardwicke & Gray, 1827 (Squamata: Scincidae) from northeastern Cambodia, with an updated identification key to the genus *Lygosoma* in mainland Southeast Asia. *Zootaxa* **3190**, 5.
- Geissmann T. (2002) Taxonomy and evolution of gibbons. *Evolutionary Anthropology: Issues, News, and Reviews* **11**, 28-31.
- Geissmann T. (2007) Status reassessment of the gibbons: results of the Asian primate red list workshop 2006. *Gibbon Journal* **3**, 5-15.
- Geissmann T., Manh Ha N., Rawson B., Timmins R. & Traeholt C. (2008) *Nomascus gabriellae*. The IUCN Red List of Threatened Species. Version 2015.2.
- Gentry A.H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, 1-34.
- Gerwing J.J., Schnitzer S.A., Burnham R.J., Bongers F., Chave J., DeWalt S.J., Ewango C.E., Foster R., Kenfack D. & Martínez-Ramos M. (2006) A Standard Protocol for Liana Censuses 1. *Biotropica* **38**, 256-61.
- Gittins S.P. & Raemaekers J.J. (1980) Siamang, lar and agile gibbons. In: *Malayan Forest Primates* (pp. 63-106. Springer.

- Givens D.I. & Shingfield K. (2004) Foods derived from animals: the impact of animal nutrition on their nutritive value and ability to sustain long-term health. *Nutrition Bulletin* **29**, 325-32.
- Glander K.E. (1982) The impact of plant secondary compounds on primate feeding behavior. *American Journal of Physical Anthropology* **25**, 1-18.
- Goodall J. (1986) The chimpanzees of Gombe: Patterns of behavior.
- Grandison R.C., Piper M.D. & Partridge L. (2009) Amino-acid imbalance explains extension of lifespan by dietary restriction in *Drosophila*. *Nature* **462**, 1061-4.
- Gray T., Phan C. & Long B. (2010) Modelling species distribution at multiple spatial scales: gibbon habitat preferences in a fragmented landscape. *Animal Conservation* **13**, 324-32.
- Gray T.N., Phan C., Pin C. & Prum S. (2012) Establishing a monitoring baseline for threatened large ungulates in eastern Cambodia. *Wildlife Biology* **18**, 406-13.
- Halfwerk W., Holleman L.J., Lessells C.K. & Slabbekoorn H. (2011) Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology* **48**, 210-9.
- Hamilton R.A. & Galdikas B.M. (1994) A preliminary study of food selection by the orangutan in relation to plant quality. *Primates* **35**, 255-63.
- Hansen M.C., Potapov P.V., Moore R., Hancher M., Turubanova S., Tyukavina A., Thau D., Stehman S., Goetz S. & Loveland T. (2013) High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850-3.
- Hanson J.D., Larson M.E. & Snowdon C.T. (1976) The effects of control over high intensity noise on plasma cortisol levels in rhesus monkeys. *Behavioral Biology* **16**, 333-40.
- Hanya G. & Bernard H. (2012) Fallback foods of red leaf monkeys (*Presbytis rubicunda*) in Danum Valley, Borneo. *International Journal of Primatology* **33**, 322-37.
- Hanya G. & Bernard H. (2015) Different Roles of Seeds and Young Leaves in the Diet of Red Leaf Monkeys (*Presbytis rubicunda*): Comparisons of Availability, Nutritional Properties, and Associated Feeding Behavior. *International Journal of Primatology*, 1-17.
- Hardus M.E., Lameira A.R., Menken S.B. & Wich S.A. (2012) Effects of logging on orangutan behavior. *Biological Conservation* **146**, 177-87.
- Harris N.L., Brown S., Hagen S.C., Saatchi S.S., Petrova S., Salas W., Hansen M.C., Potapov P.V. & Lotsch A. (2012) Baseline map of carbon emissions from deforestation in tropical regions. *Science* **336**, 1573-6.
- Harris T.R., Chapman C.A. & Monfort S.L. (2010) Small folivorous primate groups exhibit behavioral and physiological effects of food scarcity. *Behavioral Ecology* **21**, 46-56.

- Hassanin A., Ropiquet A., Cornette R., Tranier M., Pfeffer P., Candegabe P. & Lemaire M. (2006) Has the kouprey (*Bos sauveli* Urbain, 1937) been domesticated in Cambodia? *Comptes Rendus Biologies* **329**, 124-35.
- Hill J. (2011) Review of local knowledge and uses for primates in the Veun Sai-Siem Pang Conservaion Area, northeastern Cambodia. *Journal of the MSc in Primate Conservation* **12**, 9.
- Hladik C.M. (1977) Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on the diet. *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys, and Apes*, 81-501.
- Hon N., Neak P., Khov V. & Cheat V. (2010) Food and habitat of Asian small-clawed otter in northeastern Cambodia. *IUCN Otter Spec. Group Bull* **21**, 12-23.
- Htun S., Timmins R., Boonratana R. & Das J. (2008) *Macaca arctoides*. The IUCN Red List of Threatened Species. Version 2015.2.
- ICEM (2003) *Cambodia National Report on Protected Areas and Development. Review of Protected Areas and Development in the Lower Mekong River Region.*, Indooroopilly, Queensland, Australia. 148pp.
- Irwin M.T., Raharison J.L., Raubenheimer D., Chapman C.A. & Rothman J.M. (2014) Nutritional correlates of the “lean season”: effects of seasonality and frugivory on the nutritional ecology of diademed sifakas. *American Journal of Physical Anthropology* **153**, 78-91.
- Isbell L.A. & Young T.P. (1993) Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. *Behavioral Ecology and Sociobiology* **32**, 377-85.
- Islam M. & Feeroz M. (1992) Ecology of hoolock gibbon of Bangladesh. *Primates* **33**, 451-64.
- ITTO (2003) Annual review and assessment of the world timber situation, 2003. International Tropical Timber Association (ITTO).
- IUCN (2015) International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Version 2015. 1. www.iucnredlist.org. Download on 02 June 2015.
- IUCN/SSC (2013) Guideline for Reintroductions and Other Conservation Translocations. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission, Viii + 57 pp.
- Johns A.D. (1986) Effects of selective logging on the behavioral ecology of West Malaysian primates. *Ecology*, 684-94.
- Johnson A., Singh S., Duangdala M. & Hedemark M. (2005) The western black crested gibbon *Nomascus concolor* in Laos: new records and conservation status. *Oryx* **39**, 311-7.

- Johnson C., Raubenheimer D., Rothman J., Clarke D., Swedell L. & Deschner T. (2013) Days in the life: daily nutrient balancing in a wild chacma baboon. *PloS One* **8**, e70383.
- Kao D. & Iida S. (2006) Structural characteristics of logged evergreen forests in Preah Vihear, Cambodia, 3 years after logging. *Forest Ecology and Management* **225**, 62-73.
- Keo O., Collar N.J. & Sutherland W.J. (2009) Nest protectors provide a cost-effective means of increasing breeding success in giant ibis *Thaumatibis gigantea*. *Bird Conservation International* **19**, 77-82.
- King A., Behie A. & Hon N. (in review) Patterns of salt lick use by mammal and bird species in northern Cambodia.
- Kleiman D.G., Beck B.B., Dietz J.M., Dietz L.A., Ballou J.D. & Coimbra-Filho A.F. (1986) Conservation program for the golden lion tamarin: captive research and management, ecological studies, educational strategies, and reintroduction. In: *Primates* (pp. 959-79). Springer.
- Koenig A., Borries C., Chalise M.K. & Winkler P. (1997) Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). *Journal of Zoology* **243**, 215-35.
- Konrad R. (2004) Vocal Diversity and Taxonomy of the Crested Gibbons (Genus *Nomascus*) in Cambodia. Anthropological Institute and Museum, University of Zürich.
- Konrad R. & Geissmann T. (2006) Vocal diversity and taxonomy of *Nomascus* in Cambodia. *International Journal of Primatology* **27**, 713-45.
- Kool K. (1992) Food selection by the silver leaf monkey, *Trachypithecus auratus sondaicus*, in relation to plant chemistry. *Oecologia* **90**, 527-33.
- Korstjens A.H., Lehmann J. & Dunbar R. (2010) Resting time as an ecological constraint on primate biogeography. *Animal Behaviour* **79**, 361-74.
- Kumar A., Mary K. & Bagchie P. (2009) Present distribution, population status, and conservation of western hoolock gibbons Hoolock hoolock (*Primates: Hylobatidae*) in Namdapha National Park, India. *Journal of Threatened Taxa* **1**, 203-9.
- Lambrick F.H., Brown N.D., Lawrence A. & Bebbler D.P. (2014) Effectiveness of Community Forestry in Prey Long Forest, Cambodia. *Conservation Biology* **28**, 372-81.
- Lang C. (2001) Deforestation in Vietnam, Laos and Cambodia. *Deforestation, Environment, and Sustainable Development: A comparative analysis*, 111-37.
- Lappan S. (2008) Male care of infants in a siamang (*Symphalangus syndactylus*) population including socially monogamous and polyandrous groups. *Behavioral Ecology and Sociobiology* **62**, 1307-17.

- Lappan S. & Whittaker D. (2009) *The gibbons: new perspectives on small ape socioecology and population biology*. Springer Science & Business Media.
- Laska M., Salazar L.T.H. & Luna E.R. (2000) Food preferences and nutrient composition in captive spider monkeys, *Ateles geoffroyi*. *International Journal of Primatology* **21**, 671-83.
- Laval P., Rakotoarison H., Savajol N. & Vanny T. (2011) The contribution of wild medicinal plants towards poverty alleviation and health improvements: a case study in two villages in Mondulkiri Province, Cambodia. *Cambodian Journal of Natural History* **1**, 29-39.
- Le Billon P. (2000) The political ecology of transition in Cambodia 1989–1999: War, peace and forest exploitation. *Development and Change* **31**, 785-805.
- Le Billon P. (2002) Logging in Muddy Waters: The Politics of Forest Exploitation in Cambodia, *Critical Asian Studies*, 34:4, 563-586, DOI.
- Leibold M.A. & Wilbur H.M. (1992) Interactions between food-web structure and nutrients on pond organisms.
- Lengagne T. (2008) Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. *Biological Conservation* **141**, 2023-31.
- Li H., Aide T.M., Ma Y., Liu W. & Cao M. (2007) Demand for rubber is causing the loss of high diversity rain forest in SW China. *Biodiversity and Conservation* **16**, 1731-45.
- Licitra G., Hernandez T. & Van Soest P. (1996) Standardization of procedures for nitrogen fractionation of ruminant feeds. *Animal Feed Science and Technology* **57**, 347-58.
- Long H.T., Tam N.A., Minh H.T., Tinh N.T. & Van Tuan B. (2011) Survey of the northern buff-cheeked crested gibbon (*Nomascus annamensis*) in Kon Ka Kinh National Park, Gia Lai Province, Vietnam.
- Loucks C., Mascia M.B., Maxwell A., Huy K., Duong K., Chea N., Long B., Cox N. & Seng T. (2009) Wildlife decline in Cambodia, 1953–2005: Exploring the legacy of armed conflict. *Conservation Letters* **2**, 82-92.
- Lynam A.J. (2010) Securing a future for wild Indochinese tigers: Transforming tiger vacuums into tiger source sites. *Integrative Zoology* **5**, 324-34.
- Ma S., Wang Y. & Poirier F.E. (1988) Taxonomy, distribution, and status of gibbons (*Hylobates*) in southern China and adjacent areas. *Primates* **29**, 277-86.
- MacArthur R.H. & Pianka E.R. (1966) On optimal use of a patchy environment. *American Naturalist*, 603-9.

- Maldonado A.M., Nijman V. & Bearder S.K. (2009) Trade in night monkeys *Aotus* spp. In the Brazil–Colombia–Peru tri-border area: international wildlife trade regulations are ineffectively enforced. *Endangered Species Research* **9**, 143-9.
- Malhi Y., Roberts J.T., Betts R.A., Killeen T.J., Li W. & Nobre C.A. (2008) Climate change, deforestation, and the fate of the Amazon. *Science* **319**, 169-72.
- Malone N., Selby M. & Longo S. (2014) Political-Ecological Dimensions of Silvery Gibbon Conservation Efforts: An Endangered Ape in (and on) the Verge. *International Journal of Sociology* **44**, 34-53.
- Malone N.M., Fuentes A. & White F. (2010) Ethics commentary: subjects of knowledge and control in field primatology. *American Journal of Primatology* **72**, 779-84.
- Marshall J.T. & Marshall E.R. (1976) Gibbons and their territorial songs. *Science* **193**, 235-7.
- Matsuda I., Tuuga A., Bernard H., Sugau J. & Hanya G. (2013) Leaf selection by two Bornean colobine monkeys in relation to plant chemistry and abundance. *Scientific reports* **3**.
- Mattison J.A., Roth G.S., Beasley T.M., Tilmont E.M., Handy A.M., Herbert R.L., Longo D.L., Allison D.B., Young J.E. & Bryant M. (2012) Impact of caloric restriction on health and survival in rhesus monkeys from the NIA study. *Nature*.
- Mattson Jr W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual review of ecology and systematics*, 119-61.
- Mattson W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual review of ecology and systematics*, 119-61.
- McConkey K.R., Aldy F., Ario A. & Chivers D.J. (2002) Selection of fruit by gibbons (*Hylobates muelleri* × *agilis*) in the rain forests of central Borneo. *International Journal of Primatology* **23**, 123-45.
- McKenney B., Chea Y., Tola P. & Evans T. (2004) Focusing on Cambodia's high value forests: Livelihoods and management. *Cambodia Development Resource Institute and Wildlife Conservation Society, Phnom Penh*.
- Mckey D.B., Gartlan J.S., Waterman P.G. & Choo G.M. (1981) Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biological Journal of the Linnean Society* **16**, 115-46.
- McPhee M.E. (2004) Generations in captivity increases behavioral variance: considerations for captive breeding and reintroduction programs. *Biological Conservation* **115**, 71-7.
- Mead P.S., Slutsker L., Dietz V., McCaig L.F., Bresee J.S., Shapiro C., Griffin P.M. & Tauxe R.V. (1999) Food-related illness and death in the United States. *Emerging Infectious Diseases* **5**, 607.
- Medley K.E. (1993) Primate conservation along the Tana River, Kenya: an examination of the forest habitat. *Conservation Biology* **7**, 109-21.

- Milne S. & Niesten E. (2009) Direct payments for biodiversity conservation in developing countries: practical insights for design and implementation. *Oryx* **43**, 530-41.
- Milton K. (1979) Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *American Naturalist*, 362-78.
- Milton K. (1999) Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us? *Nutrition* **15**, 488-98.
- Min B. & Hart S. (2003) Tannins for suppression of internal parasites. *Journal of Animal Science* **81**, E102-E9.
- Mitrajit D., Sudip C., Indu S., Bhattacharjee P.C., Formicki G., Bulla J. & Shubhadeep R. (2014) Nutritional stress in western hoolock gibbon due to adverse changes in diet pattern. *Journal of Microbiology, Biotechnology and Food Sciences* **4**, 152-6.
- Mittermeier R. (1986) A global overview of primate conservation. *Primate Ecology and Conservation, Cambridge University Press, Cambridge*, 325-40.
- Monda K., Simmons R.E., Kressirer P., Su B. & Woodruff D.S. (2007) Mitochondrial DNA hypervariable region-1 sequence variation and phylogeny of the concolor gibbons, *Nomascus*. *American Journal of Primatology* **69**, 1285-306.
- Mootnick A.R. & Fan P.F. (2011) A comparative study of crested gibbons (*Nomascus*). *American Journal of Primatology* **73**, 135-54.
- Moser B., Schütz M. & Hindenlang K.E. (2006) Importance of alternative food resources for browsing by roe deer on deciduous trees: the role of food availability and species quality. *Forest Ecology and Management* **226**, 248-55.
- Myers N., Mittermeier R.A., Mittermeier C.G., Da Fonseca G.A. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853-8.
- Nadler T., Rawson B.M. & Thinh T.N. (2010) *Conservation of Primates in Indochina*, Frankfurt Zoological Society and Conservation International, Hanoi.
- Nadler T., Timmins R. & Richardson M. (2008) *Trachypithecus germaini*. The IUCN Red List of Threatened Species. Version 2015.2.
- Nakamura Y., Takahashi A. & Ota H. (2014) A new, recently extinct subspecies of the Kuroiwa's Leopard Gecko, *Goniurosaurus kuroiwa* (Squamata: Eublepharidae), from Yoronjima Island of the Ryukyu Archipelago, Japan. *Acta Herpetologica* **9**, 61-73.
- Nelson B. (2014) Sleeping tree selection by northern yellow-cheeked crested gibbons (*Nomascus annamensis*) in Cambodia. MSc thesis, the Australian National University, Australia.

- Ngoc Thanh V., Lippold L., Timmins R. & Manh Ha N. (2008) *Pygathrix nemaeus*. The IUCN Red List of Threatened Species. Version 2015.2.
- Ni Q.-Y., Huang B., Liang Z.-L., Wang X.-W. & Jiang X.-L. (2014) Dietary Variability in the Western Black Crested Gibbon (*Nomascus concolor*) Inhabiting an Isolated and Disturbed Forest Fragment in Southern Yunnan, China. *American Journal of Primatology* **76**, 217-29.
- Nijman V. (2001) Effects of behavioural changes due to habitat disturbance on density estimation of rain forest vertebrates, as illustrated by gibbons (primates: Hylobatidae). *Forest (and) primates: conservation and ecology of the endemic primates of Java and Borneo*, Tropenbos Foundation. Wageningen: Tropenbos International. p, 33-42.
- Nijman V. & Asia T.S. (2009) *An assessment of trade in gibbons and orang-utans in Sumatra, Indonesia*. TRAFFIC Southeast Asia Kuala Lumpur.
- Nijman V., Nekaris K., Donati G., Bruford M. & Fa J. (2011) Primate conservation: measuring and mitigating trade in primates. *Endanger Species Research* **13**, 159-61.
- Novotny V., Drozd P., Miller S.E., Kulfan M., Janda M., Basset Y. & Weiblen G.D. (2006) Why are there so many species of herbivorous insects in tropical rainforests? *Science* **313**, 1115-8.
- NRC (2003) *Nutrient requirements of nonhuman primates. 2nd rev. ed. Washington, DC: National Academy Press. 286p.*
- Núñez-Iturri G. & Howe H.F. (2007) Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in western Amazonia. *Biotropica* **39**, 348-54.
- O'Brien T.G., Kinnaird M.F., Nurcahyo A., Iqbal M. & Rusmanto M. (2004) Abundance and distribution of sympatric gibbons in a threatened Sumatran rain forest. *International Journal of Primatology* **25**, 267-84.
- O'Kelly H.J., Evans T.D., Stokes E.J., Clements T.J., Dara A., Gately M., Menghor N., Pollard E.H., Soriyun M. & Walston J. (2012) Identifying conservation successes, failures and future opportunities; assessing recovery potential of wild ungulates and tigers in eastern Cambodia. *PloS One* **7**, e40482.
- O'Malley R.C. & Power M.L. (2012) Nutritional composition of actual and potential insect prey for the Kasekela chimpanzees of Gombe National Park, Tanzania. *American journal of physical anthropology* **149**, 493-503.
- O'Kelly H.J. (2013) Monitoring Conservation Threats, Interventions and Impacts on Wildlife in a Cambodian Tropical Forest.
- Oates J.F., Abedi-Lartey M., McGraw W.S., Struhsaker T.T. & Whitesides G.H. (2000) Extinction of a West African red colobus monkey. *Conservation Biology* **14**, 1526-32.
- Oates J.F., Waterman P.G. & Choo G.M. (1980) Food selection by the south Indian leaf-monkey, *Presbytis johnii*, in relation to leaf chemistry. *Oecologia* **45**, 45-56.

- ODC (2014a) Cambodian Forest Cover maps between 1973 - 2014.
www.opendevelopmentcambodia.net/briefing/forest-cover
- ODC (2014b) Cambodian Protected Area.
www.opendevelopmentcambodia.net/briefing/protected-areas.
- Oftedal O.T., Whiten A., Southgate D. & Van Soest P. (1991) The Nutritional Consequences of Foraging in Primates: The Relationship of Nutrient Intakes to Nutrient Requirements and Discussion. *Philosophical Transactions of the Royal Society B: Biological Sciences* **334**, 161-70.
- Ong P. & Richardson M. (2008) *Macaca fascicularis*. The IUCN Red List of Threatened Species. Version 2015.2.
- Osterberg P., Samphanthamit P., Maprang O., Punnadee S. & Brockelman W.Y. (2014) Population Dynamics of a Reintroduced Population of Captive-Raised Gibbons (*Hylobates lar*) on Phuket, Thailand. *Primate Conservation*, 179-88.
- Osterberg P., Samphanthamit P., Maprang O., Punnadee S. & Brockelman W.Y. (2015) Gibbon (*Hylobates lar*) Reintroduction Success in Phuket, Thailand, and Its Conservation Benefits. *American Journal of Primatology* **77**, 492-501.
- Palo R.T. & Robbins C.T. (1991) *Plant defenses against mammalian herbivory*. CRC Press.
- Peng-Fei F., Xue-Long J. & Chang-Cheng T. (2009) The critically endangered black crested gibbon *Nomascus concolor* on Wuliang Mountain, Yunnan, China: the role of forest types in the species' conservation. *Oryx* **43**, 203-8.
- Philippart J.C. (1995) Is captive breeding an effective solution for the preservation of endemic species? *Biological Conservation* **72**, 281-95.
- Phon D. (2000) Dictionary of Plants used in Cambodia. *Imprimerie Olympic, Phnom Penh*.
- Phoonjampa R. & Brockelman W.Y. (2008) Survey of pileated gibbon *Hylobates pileatus* in Thailand: populations threatened by hunting and habitat degradation. *Oryx* **42**, 600-6.
- Pimm S.L. & Raven P. (2000) Biodiversity: extinction by numbers. *Nature* **403**, 843-5.
- Plumptre A.J. & Reynolds V. (1994) The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *Journal of Applied Ecology*, 631-41.
- Pollard E., Clements T., Hor N.M., Ko S. & Rawson B. (2007) Status and conservation of globally threatened primates in the Seima Biodiversity Conservation Area, Cambodia. *Wildlife Conservation Society, Cambodia Program, Phnom Penh, Cambodia*.
- Pontes A.R.M. & Soares M.L. (2005) Sleeping sites of common marmosets (*Callithrix jacchus*) in defaunated urban forest fragments: a strategy to maximize food intake. *Journal of Zoology* **266**, 55-63.

- Porter L.J., Hrstich L.N. & Chan B.G. (1985) The conversion of procyanidins and prodelphinidins to cyanidin and delphinidin. *Phytochemistry* **25**, 223-30.
- Price P.W., Bouton C.E., Gross P., McPherson B.A., Thompson J.N. & Weis A.E. (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual review of ecology and systematics*, 41-65.
- Putz F.E., Zuidema P.A., Synnott T., Peña-Claros M., Pinard M.A., Sheil D., Vanclay J.K., Sist P., Gourlet-Fleury S. & Griscom B. (2012) Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conservation Letters* **5**, 296-303.
- Ratner B.D. (2006) Community management by decree? Lessons from Cambodia's fisheries reform. *Society and Natural Resources* **19**, 79-86.
- Raubenheimer D. (2011) Toward a quantitative nutritional ecology: the right-angled mixture triangle. *Ecological monographs* **81**, 407-27.
- Raubenheimer D., Machovsky-Capuska G.E., Chapman C.A. & Rothman J.M. (2015) Geometry of nutrition in field studies: an illustration using wild primates. *Oecologia* **177**, 223-34.
- Raubenheimer D. & Simpson S.J. (1997) Integrative models of nutrient balancing: application to insects and vertebrates. *Nutrition research reviews* **10**, 151-79.
- Raubenheimer D. & Simpson S.J. (2004) Organismal stoichiometry: quantifying non-independence among food components. *Ecology* **85**, 1203-16.
- Rawson B. (2010a) The status of Cambodian primates. T. Nadler, B. Rawson, and Van Ngoc Thin, editors. *Conservation of Primates in Indochina. Frankfurt Zoological Society and Conservation International, Hanoi, Vietnam*, 17-26.
- Rawson B., Lippold L., Timmins R., Ngoc Thanh V. & Manh Ha N. (2008) *Pygathrix nigripes*. The IUCN Red List of Threatened Species. Version 2015.2.
- Rawson B. & Roos C. (2008) A new primate species record for Cambodia: *Pygathrix nemaus*. *Cambodian Journal of Natural History* **1**, 7-11.
- Rawson B.M. (2009) The socio-ecology of the black-shanked douc (*Pygathrix nigripes*) in Mondulkiri Province, Cambodia. PhD thesis, the Australian National University.
- Rawson B.M. (2010b) The status of Cambodian primates. *Conservation of Primates in Indochina*, 17-25.
- Rawson B.M. & Bach L.T. (2011) Preliminary observations of geophagy amongst Cambodia's Colobinae.

- Reed J.D. (1995) Nutritional toxicology of tannins and related polyphenols in forage legumes. *Journal of Animal Science* **73**, 1516-28.
- Rice W.R. (1989) Analyzing tables of statistical tests. *Evolution*, 223-5.
- Rop O., Mlcek J., Jurikova T., Neugebauerova J. & Vabkova J. (2012) Edible flowers—a new promising source of mineral elements in human nutrition. *Molecules* **17**, 6672-83.
- Rosenthal G.A. & Berenbaum M.R. (2012) *Herbivores: Their interactions with secondary plant metabolites: Ecological and Evolutionary Processes*. Academic Press.
- Rothman J.M., Chapman C.A. & Pell A.N. (2008a) Fiber-bound nitrogen in gorilla diets: implications for estimating dietary protein intake of primates. *American Journal of Primatology* **70**, 690-4.
- Rothman J.M., Chapman C.A. & Van Soest P.J. (2012) Methods in primate nutritional ecology: a user's guide. *International Journal of Primatology* **33**, 542-66.
- Rothman J.M., Dierenfeld E.S., Hintz H.F. & Pell A.N. (2008b) Nutritional quality of gorilla diets: consequences of age, sex, and season. *Oecologia* **155**, 111-22.
- Rothman J.M., Dierenfeld E.S., Molina D.O., Shaw A.V., Hintz H.F. & Pell A.N. (2006) Nutritional chemistry of foods eaten by gorillas in Bwindi Impenetrable National Park, Uganda. *American Journal of Primatology* **68**, 675-91.
- Rothman J.M., Raubenheimer D., Bryer M.A., Takahashi M. & Gilbert C.C. (2014) Nutritional contributions of insects to primate diets: implications for primate evolution. *Journal of Human Evolution* **71**, 59-69.
- Rothman J.M., Raubenheimer D. & Chapman C.A. (2011) Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. *Biology letters*, rsbl20110321.
- Russo S.E., Campbell C.J., Dew J.L., Stevenson P.R. & Suarez S.A. (2005) A multi-forest comparison of dietary preferences and seed dispersal by *Ateles spp.* *International Journal of Primatology* **26**, 1017-37.
- Ryan C.A. (1989) Proteinase inhibitor gene families: strategies for transformation to improve plant defenses against herbivores. *BioEssays* **10**, 20-4.
- Sasaki N. (2006) Carbon emissions due to land-use change and logging in Cambodia: a modeling approach. *Journal of Forest Research* **11**, 397-403.
- Schipper J., Chanson J.S., Chiozza F., Cox N.A., Hoffmann M., Katariya V., Lamoreux J., Rodrigues A.S., Stuart S.N. & Temple H.J. (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* **322**, 225-30.
- Schmidt L. & Nguyen V.A. (2005) *Dialium cochichinense* Pierre. *Seed Leaflet* **91**, 1-2.

- Schoener T.W. (1971) Theory of feeding strategies. *Annual review of ecology and systematics*, 369-404.
- Serio-Silva J.C., Rico-Gray V., Hernández-Salazar L.T. & Espinosa-Gómez R. (2002) The role of *Ficus* (Moraceae) in the diet and nutrition of a troop of Mexican howler monkeys, *Alouatta palliata mexicana*, released on an island in southern Veracruz, Mexico. *Journal of Tropical Ecology* **18**, 913-28.
- Shah N., Atallah M.T., Mahoney R.R. & Pellett P.L. (1982) Effect of dietary fiber components on fecal nitrogen excretion and protein utilization in growing rats. *J. Nutr* **112**, 658-66.
- Sharma N., Madhusudan M.D. & Sinha A. (2014) Local and Landscape Correlates of Primate Distribution and Persistence in the Remnant Lowland Rainforests of the Upper Brahmaputra Valley, Northeastern India. *Conservation Biology* **28**, 95-106.
- Shepherd C.R. (2010) Illegal primate trade in Indonesia exemplified by surveys carried out over a decade in North Sumatra. *Endangered Species Research* **11**, 201-5.
- Siemers B.M. & Schaub A. (2011) Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *Proceedings of the Royal Society of London B: Biological Sciences* **278**, 1646-52.
- Silver S.C., Ostro L.E., Yeager C. & Horwich R. (1998) Feeding ecology of the black howler monkey (*Alouatta pigra*) in northern Belize. *American Journal of Primatology* **45**, 263-79.
- Simmen B., Tarnaud L., Marez A. & Hladik A. (2013) Leaf chemistry as a predictor of primate biomass and the mediating role of food selection: A case study in a folivorous lemur (*Propithecus verreauxi*). *American Journal of Primatology*.
- Simpson S. & Raubenheimer D. (1993) A multi-level analysis of feeding behaviour: the geometry of nutritional decisions. *Philosophical Transactions of the Royal Society B: Biological Sciences* **342**, 381-402.
- Simpson S. & Raubenheimer D. (1995) The geometric analysis of feeding and nutrition: a user's guide. *Journal of Insect Physiology* **41**, 545-53.
- Slabbekoorn H. & Ripmeester E.A. (2008) Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology* **17**, 72-83.
- Smith E., A D., Husson S.J., C Y. & Harrison M.E. (2013) Feeding ecology of red langurs in Sabangau tropical peat-swamp forest, Indonesian Borneo: extreme granivory in a non-masting forest. *American Journal of Primatology* **75**, 848-59.
- Speiser B. & Rowell-Rahier M. (1991) Effects of food availability, nutritional value, and alkaloids on food choice in the generalist herbivore *Arianta arbustorum* (Gastropoda: Helicidae). *Oikos*, 306-18.

- Starr C., Nekaris K., Streicher U. & Leung L. (2010) Traditional use of slow lorises *Nycticebus bengalensis* and *N. pygmaeus* in Cambodia: an impediment to their conservation. *Endangered Species Research* **12**, 17-23.
- Starr C., Nekaris K., Streicher U. & Leung L.K.-P. (2011) Field surveys of the Vulnerable pygmy slow loris *Nycticebus pygmaeus* using local knowledge in Mondulkiri Province, Cambodia. *Oryx* **45**, 135-42.
- Stevenson P.R. (2000) Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: Dispersal distance, germination rates, and dispersal quantity. *American Journal of Primatology* **50**, 275-89.
- Stevenson P.R., Castellanos M.C., Pizarro J.C. & Garavito M. (2002) Effects of seed dispersal by three ateline monkey species on seed germination at Tinigua National Park, Colombia. *International Journal of Primatology* **23**, 1187-204.
- Streicher U., Ngoc Thanh V., Nadler T., Timmins R. & Nekaris A. (2008a) *Nycticebus*. The IUCN Red List of Threatened Species. Version 2015. 2.
- Streicher U., Singh M., Timmins R. & Brockelman W. (2008b) *Nycticebus bengalensis*. The IUCN Red List of Threatened Species. Version 2015. 2.
- Strier K.B. (1992) Atelinae adaptations: behavioral strategies and ecological constraints. *American Journal of Physical Anthropology* **88**, 515-24.
- Strier K.B. (2007) *Primate behavioral ecology*. Allyn and Bacon Boston.
- Sutherland W.J. (1998) The importance of behavioural studies in conservation biology. *Animal Behaviour* **56**, 801-9.
- Taylor S.S., Jamieson I.G. & Armstrong D.P. (2005) Successful island reintroductions of New Zealand robins and saddlebacks with small numbers of founders. *Animal Conservation* **8**, 415-20.
- Te Wong S., Servheen C., Ambu L. & Norhayati A. (2005) Impacts of fruit production cycles on Malayan sun bears and bearded pigs in lowland tropical forest of Sabah, Malaysian Borneo. *Journal of Tropical Ecology* **21**, 627-39.
- Terborgh J. (1986) Community aspects of frugivory in tropical forests. In: *Frugivores and seed dispersal* (pp. 371-84. Springer.
- Thévenon S., Bonnet A., Claro F. & Maillard J.C. (2003) Genetic diversity analysis of captive populations: The Vietnamese sika deer (*Cervus nippon pseudaxis*) in zoological parks. *Zoo Biology* **22**, 465-75.
- Thinh V., Ngoc, R A., Thanh V.N., Nadler T. & Roos C. (2010) A new species of crested gibbon, from the central Annamite mountain range. *Vietnamese Journal of Primatology* **1**, 1-12.

- Thompson M.E. & Wrangham R.W. (2008) Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. *American Journal of Physical Anthropology* **135**, 171-81.
- Traeholt C., Bonthoeun R., Virak C., Samuth M. & Vutthin S. (2006) Song Activity of the Pileated Gibbon, *Hylobates pileatus*, in Cambodia. *Primate Conservation*, 139-44.
- Trepanowski J.F., Canale R.E., Marshall K.E., Kabir M.M. & Bloomer R.J. (2011) Impact of caloric and dietary restriction regimens on markers of health and longevity in humans and animals: a summary of available findings. *Nutr J* **10**, 10.1186.
- Tutin C.E., Ancrenaz M., Paredes J., Vacher-Vallas M., Vidal C., Goossens B., Bruford M.W. & Jamart A. (2001) Conservation Biology Framework for the Release of Wild-Born Orphaned Chimpanzees into the Conkouati Reserve, Congo. *Conservation Biology* **15**, 1247-57.
- Van Soest P.J. (1978) Dietary fibers: their definition and nutritional properties. *The American Journal of Clinical Nutrition* **31**, S12-S20.
- Van Soest P.v., Robertson J. & Lewis B. (1991) Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* **74**, 3583-97.
- Vedder A.L. (1984) Movement patterns of a group of free-ranging mountain gorillas (*Gorilla gorilla beringei*) and their relation to food availability. *American Journal of Primatology* **7**, 73-88.
- Veeramah K.R., Woerner A.E., Johnstone L., Gut I., Gut M., Marques-Bonet T., Carbone L., Wall J.D. & Hammer M.F. (2015) Examining Phylogenetic Relationships Among Gibbon Genera Using Whole Genome Sequence Data Using an Approximate Bayesian Computation Approach. *Genetics* **200**, 295-U575.
- Vinh L.Q., Tinh V.T., Hai D.T., Do Quang Huy N.D.M. & Trinh B.H. (2010) Survey of Northern Buff-cheeked Crested Gibbon (*Nomascus annamensis*) in Kon Cha Rang Nature Reserve.
- Walston J., Robinson J.G., Bennett E.L., Breitenmoser U., da Fonseca G.A., Goodrich J., Gumal M., Hunter L., Johnson A. & Karanth K.U. (2010) Bringing the tiger back from the brink—the six percent solution. *PLoS Biology* **8**, e1000485.
- Wasserman M.D. & Chapman C.A. (2003) Determinants of colobine monkey abundance: the importance of food energy, protein and fibre content. *Journal of Animal Ecology* **72**, 650-9.
- Watanuki Y. & Nakayama Y. (1993) Age difference in activity pattern of Japanese monkeys: effects of temperature, snow, and diet. *Primates* **34**, 419-30.
- WCS (2009) List of animal on the IUCN Red List Found in Cambodia. Wildlife Conservation Society - Cambodia Program, Phnom Penh.

- Wells D.L. (2005) A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science* **93**, 13-7.
- Wendeln M.C., Runkle J.R. & Kalko E.K. (2000) Nutritional Values of 14 Fig Species and Bat Feeding Preferences in Panama1. *Biotropica* **32**, 489-501.
- Westoby M. (1974) An analysis of diet selection by large generalist herbivores. *American Naturalist*, 290-304.
- Whiten A., Byrne R., Barton R., Waterman P., Henzi S., Hawkes K., Widdowson E., Altmann S., Milton K. & Dunbar R. (1991) Dietary and foraging strategies of baboons [and discussion]. *Philosophical Transactions of the Royal Society B: Biological Sciences* **334**, 187-97.
- Whittington C. & Treesucon U. (1991) Selection and treatment of food plants by white-handed gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand. *Natural History Bulletin of the Siam Society* **39**, 111-22.
- Whitmore T.C. & Burnham C.P. (1975) *Tropical Rain Forests of the Far East*. Clarendon Press.
- Wickramagamage P. (1998) Large-scale deforestation for plantation agriculture in the hill country of Sri Lanka and its impacts. *Hydrological Processes* **12**, 2015-28.
- Wiederholt R. & Post E. (2010) Tropical warming and the dynamics of endangered primates. *Biology Letters* **6**, 257-60.
- Wittstock U., Agerbirk N., Stauber E.J., Olsen C.E., Hippler M., Mitchell-Olds T., Gershenzon J. & Vogel H. (2004) Successful herbivore attack due to metabolic diversion of a plant chemical defense. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 4859-64.
- Woodford M.H., Butynski T.M. & Karesh W.B. (2002) Habituating the great apes: the disease risks. *Oryx* **36**, 153-60.
- Wrangham R. & Waterman P. (1983) Condensed tannins in fruits eaten by chimpanzees. *Biotropica*, 217-22.
- Wrangham R.W., Chapman C.A. & Chapman L.J. (1994) Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology* **10**, 355-68.
- Yepez P., De La Torre S. & Snowdon C.T. (2005) Interpopulation differences in exudate feeding of pygmy marmosets in Ecuadorian Amazonia. *American Journal of Primatology* **66**, 145-58.
- Yiming L. (2006) Seasonal variation of diet and food availability in a group of Sichuan snub-nosed monkeys in Shennongjia Nature Reserve, China. *American Journal of Primatology* **68**, 217-33.

Zhang X., Wu J., Zhou W., Lin R. & Li J. (2008) Diet and time budget of hoolock gibbon (*Hoolock hoolock*) at Nankang, Gaoligongshan mountains in spring. *Sichuan Journal of Zoology* **27**, 193-6.

Appendix

Appendix 1: Social activities

Social activities were categorised as:

1. Calling was recorded whenever the sound of each gibbon was heard. The sound from each individual was different, and was easily recognized.
2. Copulation was recorded whenever the adult male and female showed sexual interaction.
3. Grooming was recorded whenever the focal animal was observed grooming another.
4. Playing was recorded whenever the focal animal was observed playing within the group members.

Appendix 2: Logging activities and food items



Figure 1a: A fresh remaining of an illegal logged tree (unidentified species) along the way to Veun Sai-Siem Pang Conservation Area (VSSPCA), northern Cambodia.

Photo: Naven Hon



Figure 1b: Another sign of illegal logging in Veun Sai-Siem Pang Conservation Area (VSSPCA), northern Cambodia.

Photo: Naven Hon



Figure 2: Unidentified insect larva eaten by the gibbons

Photo: Naven Hon

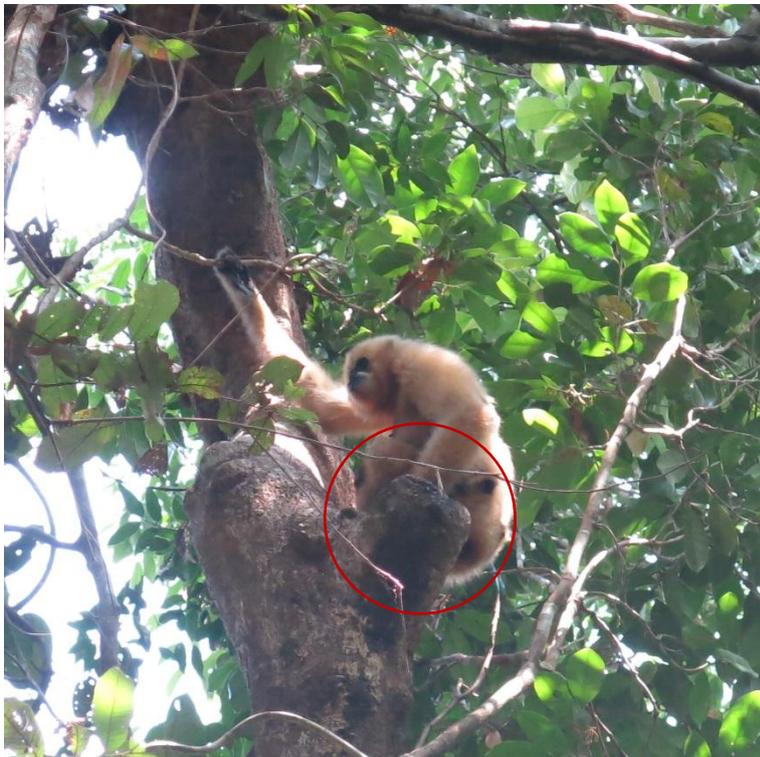


Figure 3: The adult female gibbon using her hand to get water from the cavity in the tree hole.

Photo: Naven Hon



Figure 4: A seed, was spat out after its flesh, was consumed by gibbons
Photo: Naven Hon



Figure 5: Unripe fruit of *I. umbellulata*
Photo: Naven Hon



Figure 6: Mature fruit of *A. grandis* and its tree, which bears some of fruits during the study periods.
Photo: Naven Hon



Figure 7: Leaves of large epiphyte, which were chewed and sucked by *N. annamensis*

Photo: Naven Hon



Figure 8: The remaining ripe fruit of *W. edulis* consumed the study group of *N. annamensis*, and green fruit of the same liana species, but was not consumed by this group of gibbons.

Photo: Naven Hon



Figure 9: Young leaves of *M. duperreana* were collected for samples analyses and consumed by the study group of *N. annamensis*, this tree species provides a good source for protein.

Photo: Naven Hon

Appendix 3: Rescues of baby northern yellow-cheeked crested gibbons (*N. annamensis*)



Figure 1: A baby northern yellow-cheeked crested gibbon (*Nomacrus annamensis*) was found alone in the jungle then brought to the base camp, fed with human formula milk. It does not belong to the study group of gibbons.

Photo: N. Hon and Sy sovath.



Figure 2: A law enforcement team (Forestry Administration official and military police, cooperated with Conservation International) at Veun Sai-Siem Pang Conservation Area, and MSc student from Victor University of Wellington handed baby *N. annamensis* to a Forestry Administration official and the military police from Wildlife Alliance. These officials transferred the baby to the Phnom Tamao Wildlife Recuse Centre.

Photo: Puthy Kong

Appendix 4: Statistical pairwise comparison

Table 1: Results of Mann-Whitney *U* tests comparing each individual gibbon's activities

Gibbons	Pair activities	<i>Z</i>	<i>U</i>	<i>P</i> value
Adult female	Feeding and Resting	-1.32	32	0.18
	Feeding and Travelling	3.43	4	0.0005
	Feeding and social activities	3.74	0	0.0001
	Resting and Travelling	3.66	1	0.0001
	Resting and social activities	3.74	0	0.0001
	Travelling and social activities	3.74	0	0.0001
Adult male	Feeding and Resting	0.18	47	0.84
	Feeding and Travelling	3.06	9	0.002
	Feeding and social activities	3.74	0	0.0001
	Resting and Travelling	3.36	5	0.0007
	Resting and social activities	3.74	0	0.0001
	Travelling and social activities	3.74	0	0.0001
Sub-adult male	Feeding and Resting	-1.77	26	0.07
	Feeding and Travelling	1.85	25	0.06
	Feeding and social activities	3.74	0	0.0001
	Resting and Travelling	3.28	6	0.001
	Resting and social activities	3.74	0	0.0001
	Travelling and social activities	3.74	0	0.0001
Juvenile male	Feeding and Resting	0.34	45	0.72
	Feeding and Travelling	-2.49	14	0.01
	Feeding and social activities	3.66	1	0.0002
	Resting and Travelling	2.75	13	0.0005
	Resting and social activities	3.66	1	0.0002
	Travelling and social activities	3.21	7	0.001

Table 2: Results of Mann-Whitney *U* tests comparing each individual gibbon's food choices

Gibbons	Pair activities	<i>Z</i>	<i>U</i>	<i>P</i> value
Adult female	Fruit and young leaves	2.81	2	0.004
	Fruit and Flowers	2.51	5	0.01
	Fruit and Mature leaves	2.82	8	0.004
	Young leaves and Flowers	1.20	33.5	0.22
	Young leaves and mature leaves	2.26	19.5	0.02
	Flowers and mature leaves	0.83	38.5	0.4
Adult male	Fruit and young leaves	2.88	4	0.003
	Fruit and Flowers	3.30	0	0.0009
	Fruit and Mature leaves	3.09	2	0.001
	Young leaves and Flowers	1.62	28	0.10
	Young leaves and mature leaves	2.30	19	0.02
	Flowers and mature leaves	0.34	45	0.72
Sub-adult male	Fruit and young leaves	2.72	13.5	0.006
	Fruit and Flowers	2.72	13.5	0.006
	Fruit and Mature leaves	3.32	5.5	0.0008
	Young leaves and Flowers	0.68	40.5	0.49
	Young leaves and mature leaves	2.49	16.5	0.01
Juvenile	Flowers and mature leaves	1.58	28.5	0.11
	Fruit and young leaves	2.83	12	0.004
	Fruit and Flowers	3.43	4	0.0009
	Fruit and Mature leaves	3.74	0	0.0001
	Young leaves and Flowers	2.03	23	0.04
	Young leaves and mature leaves	2.91	11	0.003
	Flowers and mature leaves	1.24	33	0.21

