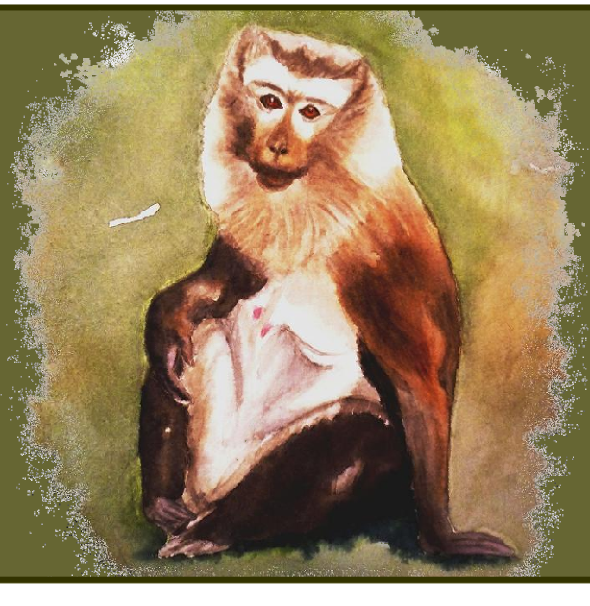
Faculté des Sciences
Département de Biologie, Ecologie et Environnement
Unité de Biologie du Comportement, Ethologie et Psychologie Animale

Feeding and ranging behavior of northern pigtailed macaques (*Macaca leonina*): impact on their seed dispersal effectiveness and ecological contribution in a tropical rainforest at Khao Yai National Park, Thailand

~ ~ ~

Régime alimentaire et déplacements des macaques à queue de cochon (*Macaca leonina*) : impact sur leur efficacité dans la dispersion des graines et sur leur contribution écologique dans une forêt tropicale du parc national de Khao Yai, Thaïlande



Année académique 2011-2012

Dissertation présentée par
Aurélie Albert
en vue de l'obtention du grade de
Docteur en Sciences

Faculté des Sciences
Département de Biologie, Ecologie et Environnement
Unité de Biologie du Comportement, Ethologie et Psychologie Animale

Feeding and ranging behavior of northern pigtailed macaques (*Macaca leonina*): impact on their seed dispersal effectiveness and ecological contribution in a tropical rainforest at Khao Yai National Park, Thailand

~ ~ ~

Régime alimentaire et déplacements des macaques à queue de cochon (*Macaca leonina*) : impact sur leur efficacité dans la dispersion des graines et sur leur contribution écologique dans une forêt tropicale du parc national de Khao Yai, Thaïlande

Année académique 2011-2012

Dissertation présentée par
Aurélie Albert
en vue de l'obtention du grade de
Docteur en Sciences

Promotrice : Marie-Claude Huynen (ULg, Belgique)

Comité de thèse : Tommaso Savini (KMUTT, Thaïlande)
Alain Hambuckers (ULg, Belgique)
Pascal Poncin (ULg, Belgique)

Président du jury : Jean-Marie Bouquegneau (ULg, Belgique)

Membres du jury : Pierre-Michel Forget (MNHN, France)
Régine Vercauteren Drubbel (ULB, Belgique)
Roseline C. Beudels-Jamar (IRSN, Belgique)

Abstract

Southeast Asia experiences an exceptional loss of natural habitat due to a deforestation rate that strongly increased during the last decades. The first consequence is the loss of many animal and plant species, threatened by their habitat degradation and by the loss of interactions necessary to the survival of the whole ecosystem. Large mammals and birds populations, the principal dispersal agent of some plant species, already collapsed massively due to hunting and habitat fragmentation and now threaten to die out. Among the large frugivorous species, primates are particularly vulnerable. Only few species, such as macaques, are able to survive in some man-made habitats, due to their opportunistic life-style. But, in the long term, habitat destruction, hunting and capture for local trade threaten their survival. The extinction of primates in Southeast Asian forests would be disastrous for many plant species as primates are among the major seed-dispersal agents.

The study of *Macaca*, the only Cercopithecinae genus in Southeast Asia, could provide a better understanding of the role of cheek-pouched monkeys in tropical rainforest maintenance and restoration. In this study, we chose to focus on northern pigtailed macaques (*Macaca leonina*) as few studies were carried out on this species, making data concerning its ecology and behavior highly limited. Their seed dispersal capacity, although unknown, is potentially high and pigtailed macaques could be as good seed dispersers as sympatric frugivores. They seem to eat a large number of fruits of many plant species, process seeds with care, and range daily over large areas. Moreover they could have a role in forest maintenance and regeneration given that they seem to eat species with all seed sizes, belonging to all plant life forms present in the forest, and they are able to cross various habitat types (primary as well as secondary forests).

After providing an outline of our current knowledge on seed dispersal by Cercopithecinae species and their specific role in forest regeneration, our aim was to highlight the importance of northern pigtailed macaques on seed dispersal and thus on forest regeneration by studying (1) how their eco-ethological characteristics can make them effective dispersers, from a quantitative and a qualitative point of view, (2) how the influence of biotic factors, such as resources and predation, on their activities and movements may impact their seed dispersal effectiveness, and (3) what role *Macaca* spp. can have in a seed dispersal assemblage.

While following a troop of northern pigtailed macaques habituated to humans in Khao Yai National Park, Thailand, we recorded their behavior, travels, and consumed items, from

dawn to dusk. Moreover, we studied the spatio-temporal distribution of fruits included in their diet, and the characteristics of their sleeping sites. Finally, we performed germination and viability tests on ingested seeds.

Results showed that northern pigtailed macaques could disperse thousands of seeds, up to 58 mm in length, coming from the 126 fruit species they eat. Especially, they could disperse them from primary to secondary forest, thanks to handling techniques such as swallowing, spitting and dropping. Finally, the seed passage through their digestive tract mostly had a neutral or positive effect on seed germination and viability. Macaques observed in this study satisfied therefore most requirements defining effective seed dispersers in both quantitative and qualitative terms and we can conclude to the potential importance of *Macaca leonina* in the tropical rainforest regeneration.

To confirm the seed dispersal effectiveness of *M. leonina*, we needed to make sure that its ranging behavior did not negatively affect dispersed seeds. Moreover, given the importance of human food in their diet, we wondered if this resource had a negative impact on seed dispersal. Our results showed that northern pigtailed macaques adapted their ranging pattern according to fruit availability. Moreover, during fruit scarcity, they shifted their diet from frugivorous to omnivorous with an important part of human food. However, human food did not seem to have an impact on seed dispersal in high fruit abundance periods where macaques had a large home range, traveled long distances and ate mainly fruits. However, in low fruit abundance periods, macaques decreased their home range size, traveled shorter distances and ate mainly human food. This latter could have a negative impact on the seed dispersal of some rare fructifying species. However, these species were eaten by many other animal species able to provide good dispersal services.

Then, we showed that sleeping sites characteristics and pre-sleep behavior in *M. leonina* were influenced by the proximity of resources and the risk of predation. Given that macaques used few sleeping sites, defecated when they woke up and that all troop members slept concentrated in a small area, we think that they created a high seed density below the sleeping trees. This may be harmful for some seed species but may be beneficial for the ecosystem. Moreover, this pattern may be shown in other effective seed dispersers in the park. So as harmful for seeds it may be, it does not make pigtailed macaques less effective than other frugivores.

Finally, we demonstrated that *Macaca* species are important associates in the seed dispersal assemblage found in Southeast Asian forests. Indeed they may disperse most plant species, usually more efficiently dispersed by other frugivores, and thus provide a significant complement in term of dispersal quantity. Moreover, they are sometimes the only frugivores able to disperse the seeds of some species, mainly large-seeded and/or protected ones, and may thus bring them a vital dispersal service.

Résumé

La forte augmentation du taux de déforestation durant les dernières décennies a engendré une perte exceptionnelle d'habitat en Asie du sud-est. La première conséquence est la perte de nombreuses espèces animales et végétales, menacée par la dégradation de leur habitat et par la perte des interactions nécessaires à la survie de tout l'écosystème. Les populations de grands mammifères et oiseaux, agents de dispersion principaux de certaines espèces végétales, ont déjà fortement diminué en raison de la chasse et de la fragmentation de l'habitat, et sont désormais menacé d'extinction. Parmi les espèces de grands frugivores, les primates sont particulièrement vulnérables. Seules quelques espèces, telles que les macaques, sont capables de survivre dans des habitats façonnés par l'Homme, en raison de leur mode de vie opportuniste. Mais, à long terme, la destruction de leur habitat, la chasse et les captures pour le commerce local menacent leur survie. L'extinction des primates dans les forêts du sud-est asiatique serait désastreuse pour de nombreuses espèces végétales étant donné qu'ils font parti des principaux agents de dispersion des graines.

L'étude des macaques, le seul genre de Cercopithecinae présent en Asie du sud-est, pourrait fournir une meilleure compréhension du rôle des singes à poches jugales dans le maintien et la restauration des forêts tropicales. Nous avons choisi de focaliser notre étude sur les macaques à queue de cochon du Nord (*Macaca leonina*) car peu d'études ont été effectuées sur cette espèce, rendant très limitées les données concernant son écologie et son comportement. Leur capacité à disperser les graines, bien qu'inconnue, est potentiellement élevée et les macaques à queue de cochon pourraient être d'aussi bons disperseurs que les frugivores sympatriques. Ils semblent manger beaucoup de fruits de nombreuses espèces, manipuler les graines avec précautions, et se déplacent chaque jour sur de grandes étendues. De plus, ils pourraient avoir un rôle dans le maintien et la régénération des forêts étant donné qu'ils semblent manger des espèces produisant des graines de toutes tailles, appartenant à tous types de plantes et qu'ils sont capables de traverser divers types d'habitats (les forêts primaires autant que les forêts secondaires).

Après avoir fourni un aperçu de nos connaissances actuelles sur la dispersion des graines par les espèces de Cercopithecinae et leur rôle spécifique dans la régénération de la forêt, notre but était de souligner l'importance des macaques à queue de cochon du Nord dans la dispersion des graines, et donc dans la régénération des forêts en étudiant (1) comment leur caractéristiques éco-éthologiques peuvent faire d'eux des disperseurs efficaces, d'un point de vue quantitatif et qualitatif, (2) comment l'influence des facteurs biotiques, telles que les

ressources et la prédation, sur les activités et leurs déplacements peut influer sur leur efficacité en tant que disperseurs de graines, et (3) quel rôle les espèces de *Macaca* peuvent avoir dans un réseaux de disperseurs de graines.

Pendant que nous suivions une troupe de macaques à queue de cochon du Nord habitués à l'Homme dans le parc national de Khao Yai, Thaïlande, nous avons enregistré leur comportement, leurs déplacements et les items qu'ils consommaient, du matin au soir. De plus, nous avons étudié la distribution spatio-temporelle des fruits inclus dans leur régime alimentaire, et les caractéristiques de leurs sites dortoirs. Finalement, nous avons testé le potentiel de germination et la viabilité des graines ingérées.

Les résultats ont montré que les macaques à queue de cochon du Nord pouvaient disperser des milliers de graines mesurant jusqu'à 58 mm et venant des 126 espèces de fruits qu'ils mangeaient. En particulier, ils pouvaient disperser ces graines de forêt primaire en forêt secondaire, grâce diverses techniques de manipulation telles que la défécation, le recrachage et le dépôt. Finalement, le passage des graines à travers leur tractus digestif avait un effet majoritairement neutre ou positif sur la germination et la viabilité de ces graines. Les macaques observés dans cette étude satisfont donc à la plupart des conditions requises pour être des disperseurs de graines efficaces en termes de quantité et de qualité, et nous pouvons conclure à l'importance potentielle de *Macaca leonina* dans la régénération de la forêt tropicale.

Pour confirmer l'efficacité de *M. leonina* en tant que disperseur de graine, nous avions besoin d'être sûrs que ses déplacements n'affectaient pas négativement les graines dispersées. De plus, étant donné l'importance de la nourriture humaine dans leur régime alimentaire, nous nous sommes demandé si cette ressource avait un effet négatif sur la dispersion des graines. Nos résultats ont montré que les macaques à queue de cochon du Nord adaptaient leurs déplacements en fonction de la disponibilité en fruits. De plus, pendant les périodes de raréfaction de fruits, ils changeaient leur régime pour passer de frugivores à omnivores avec une part importante de nourriture humaine. Cependant, cette dernière ne semblait pas avoir d'impact sur la dispersion des graines en périodes de forte abondance de fruits, quand les macaques avaient un grand domaine vital, se déplaçaient sur de longues distances et mangeaient principalement des fruits. Cependant, pendant les périodes de faible abondance de fruits, les macaques diminuaient la taille de leur domaine vital, se déplaçaient sur de plus courtes distances et mangeaient principalement de la nourriture humaine. Celle-ci pourrait donc avoir un impact négatif sur la dispersion des graines des rares espèces fructifiant à cette période. Cependant, ces espèces étaient aussi mangeaient par de nombreuses autres espèces animales capables de fournir de bons services de dispersion de graines.

Ensuite nous avons montré que les caractéristiques des sites doroirs et les comportements liés au sommeil de *M. leonina* étaient influencés par la proximité des ressources et le risque de prédation. Etant donné que les macaques utilisaient peu de sites dortoirs, déféquaient au réveil et que tous les membres de la troupe dormaient concentrés sur une petite surface, nous pensons qu'ils produisaient une forte densité de graines sous les arbres dortoirs. Ce peut être néfaste à certaines espèces de graines mais bénéfique à l'écosystème. De plus, ce pattern est observé chez d'autres disperseurs efficaces dans le parc. Ainsi, aussi néfaste pour les graines qu'il soit, ce pattern ne fait pas pour autant des macaques à queue de cochon une espèce moins efficace que les autres frugivores.

Finalement, nous avons démontré que les macaques étaient d'importants associés dans les réseaux de disperseurs présents en Asie du sud-est. En effet, ils peuvent disperser de nombreuses espèces, bien que souvent plus efficacement dispersées par d'autres frugivores, et ainsi fournir un complément significatif en termes de quantité de graines dispersées. De plus, ils sont parfois les seuls frugivores capables de disperser les graines de certaines espèces, principalement celles à larges graines et/ou munies d'une protection, et peuvent ainsi leur apporter un service de dispersion vital.

A ma mère,
A mon père

Remerciements - Acknowledgments

Je voudrais tout d'abord adresser mes plus sincères remerciements à celle sans qui rien n'aurait été possible : Marie-Claude Huynen. Tu m'as donné la chance de réaliser un rêve et tu m'as soutenue et aidée pendant toute cette aventure.

Je remercie aussi Tommaso Savini pour m'avoir guidée et conseillée, dans ma thèse tout autant que dans les méandres administratifs thaïs.

Merci à Alain Hambuckers pour le partage de vos connaissances botaniques, tous vos conseils et votre aide nécessaires à la réalisation de cette thèse.

Merci à Pascal Poncin pour m'avoir ouvert les portes de l'Unité de Biologie du comportement de l'Université de Liège.

Je remercie aussi Pierre-Michel Forget, Régine Vercauteren Drubbel et Roseline C. Beudels-Jamar pour avoir accepté d'évaluer cette thèse, et Jean-Marie Bouquegneau pour me faire l'honneur d'être le président de ce jury.

I would like to express my gratitude to George Gale and your legendary kindness for welcoming me in your lab at KMUTT and allowing me to stay at the research station at Khao Yai.

I would also like to thank Warren Brockelman for inviting me to see your seeds collection (the biggest I have ever seen!) and for your collaboration by sharing your invaluable data with me.

Many thanks to the KMUTT and Mahidol people who accompanied me and helped me to better understand the amazing Thai culture: especially Soy for having made me feel less different in your so different country; Phet (my special roommate!), Orr, Mong, Gib (my other special roommate), Dtoon and Andy for your sympathy, your help and your presence at Khao Yai; Khieo and Tim for your patience in helping me to identify all these depressing seeds! Jib for sharing your data with me and for your help in some methodological problems; Id, Rung, and June for your cheerfulness; Anuttara for kindly sharing your data with me.

Thank you Juanma for sharing and understanding what I lived. Good luck for your PhD. You will bring us wonderful data on macaques!

I thank my field assistants: At, Jak and especially Sak for your continued assistance and your always good mood. I would never have so many data without your help.

Merci à Philippe Lejeune et Lieven Devreese pour leur aide concernant la création des grilles d'échantillonnage.

I would like to thank many people for our exciting discussions on macaques, animal behavior, plants and more generally nature. Special thanks to Norberto Asensio, Shumpei Kitamura, Kim McConkey, Richard Corlett and Stephen Elliott.

I am grateful to Richard Corlett, Kim McConkey, Andreas Koenig, Carola Borries, George Gale, Paul A. Garber, and Lee Olsen for reviewing the initial manuscripts of this research.

Un grand merci à Alice et Laurence. Vous m'avez apporté de précieux conseils et avez toujours été là pour m'aider.

Merci aussi à Fany et Adeline pour votre gentillesse et votre présence à mes côtés lors de mes venues à Liège.

I want to add a word to the memory of Dr. David H. Reed who managed to make me laugh with statistics. You will miss many people.

Je tiens à remercier mes parents pour leur soutien (autant moral que financier), leurs encouragements, leurs visites en Thaïlande, ainsi que pour toutes ces bonnes choses que vous m'avez faites parvenir afin que la petite française que je suis tienne le coup dans ce pays lointain. Un grand merci aussi à ma maman pour la magnifique aquarelle située en couverture !

Un merci particulier à Lionel pour ta patience et ta compréhension, à la hauteur de ton amour pour moi.

Merci à mes sœurs, Delphine et Eléonore, pour votre soutien. Vous avez toujours cru en moi.

Merci aussi à Julie pour avoir toujours su trouver les mots justes, dans les bons moments, comme dans les plus durs.

Grâce à vous tous, malgré toutes les difficultés rencontrées, j'ai tenu le coup.

Merci à l'Université de Liège pour m'avoir accordée le prix Marie-Louise Léonard qui m'a permis de souffler un petit mois au milieu de ces quatre années…

Et bien sûr, je me dois de remercier la troupe HQ! Ces macaques qui m'en ont fait voir de toutes les couleurs mais qui vont finalement me manquer.

Table of contents

List of figures

INTRODUCTION

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

List of Boxes, Tables, and Appendices

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

1. An alarming ecological situation

1. An alarming ecological situation

1.1 Biodiversity and deforestation

Southeast Asia includes the 3rd hottest biodiversity hotspot: the **Indo-Burma region**. This area features exceptional concentrations of endemic species but experiences exceptional loss of habitat (Myers et al. 2000). Indeed, deforestation strongly increased during the last decades and only less than half (41.3-44.2%) of the primary forest was still visible in 2004. If the current rate of deforestation is maintained, Southeast Asia could lose three-quarters of its original forest by the next century (Sodhi et al. 2004). The first consequence could be the **loss of more than 40% of animal and plant species** in this area during the 21st century (Brook et al. 2003). Large mammals and birds populations already collapsed massively due to hunting and habitat fragmentation, and now they threaten to die out (Corlett 2007; Corlett 2002; Peres 2000).

Animal and plant populations are directly threatened by **deforestation** and **fragmentation** limiting their habitat, and indirectly by the **loss of interactions** between living organisms necessary to the survival of the whole ecosystem (Bleher 2000). Large frugivores are among the first affected by this loss of habitat because they need more food and larger foraging areas and tend to occur at lower densities than ecologically similar small species do, they mature later and reproduce more slowly than small species, and they tend to be preferred by hunters and, therefore, are subject to heavy hunting pressure (Johns & Skorupa 1987; p.168). Consequently, the principal **dispersal agents** of some plant species disappears (Cordeiro & Howe 2001).

1.2 What about primates?

Among the large frugivorous species, primates are particularly **vulnerable** (Chapman et al. 2003; Estrada & Coates-Estrada 1996; Johns & Skorupa 1987; Onderdonk 2000). Johns and Skorupa (1987) have shown that the percentage of fruit and flowers in the diet (in primary forest) and the survival ratios of primates were strongly negatively correlated. Southeast Asia possesses a large number of primate species and primate endemics, most being confined to intact forest (Johns & Skorupa 1987). Only a few species, such as macaques, are able to survive in some man-made habitats, due to their opportunistic life-style (Johns & Skorupa 1987). But, in the long term, **habitat destruction**, **hunting** and **capture** for local trade threaten their survival (Humphrey & Bain 1990). The extinction of primates in southeast Asian forests would be disastrous for many plant species since primates are considered as part of the **major mammalian seed-dispersal agents** (Corlett 2002).

2. Succession and dispersal

2. Succession and dispersal

2.1 Succession

Tropical forests are **dynamic systems** exhibiting both temporal and spatial variations in their ecology (Cowlishaw & Dunbar 2000) and the composition and structure of species may be affected by these directional changes (Barbour et al. 1999). Thus, in some plant communities, while the abundance of many species declines, sometimes up to their disappearance from the area, the abundance of other species, more invasive, increases. Such transitory communities are named **successional communities** (Barbour et al. 1999) and the sequence of these successional communities, replacing each other in an area, is called **succession** (Barbour et al. 1999). The ultimate stage of a succession is observed when the communities do not show any more directional change for centuries. Then, they are considered in balance with their environment and are called **climax communities** (Barbour et al. 1999).

Succession induces a continuum between each successional community and it is thus difficult to make a distinction between **primary** and **secondary forests** (Corlett 1994). In this thesis, climax forests will be considered as primary forests given they do not show any more sign of previous degradation and have the same intra-ecosystem dynamics as intact forests. On the contrary, earlier successional communities will be considered as secondary forests. They were previously degraded and still carry an obvious signs of this degradation. Their structure, as well as their composition, differs clearly from primary or climax forests (de Jong et al. 2001). During the last decades, a significant part of primary forests has been used to provide areas for forest agriculture or human settlements (Sodhi et al. 2004; Wright & Muller-Landau 2006). However, when these areas are abandoned, they may return to forest after several succession stages, turning then from secondary forests to climax forests.

During the first succession stages, ground temperature and dryness are higher due to the lack of plant cover. Plant succeeding under these extreme conditions must be sun- and dryness-tolerant species. The growth of these **pioneer species** – mainly grasses and shrubs (Benitez-Malvido 2006) – allows the progressive closing of the plant cover and, thus, the establishment of **shade-tolerant species**. As shade and moisture gain the forest, other species – mainly trees, lianas, epiphytes and hemi-epiphytes (Benitez-Malvido 2006) – establish and replace the pioneer species. Species of primary (shade-tolerant species) and secondary (pioneer species) forests differ not only by their vegetative system but also by their reproduction (Box I.1).

Box I.1 Usual characteristics of primary (shade-tolerant) *vs* secondary (pioneer) plant species

	Primary	**Secondary**
Growth	Slow	Rapid
Life span	Up to 100s years	Maximum 7-25 years
Size	Large	Small
Seed size	Large	Small
Dispersal	Zoochory (large animals)	Anemochory, Zoochory (small animals)

(Corlett & Hau 2000; Finegan 1996; Murali 1997; Wunderle 1997)

2.2 Seed dispersal: a necessary process to succession

2.2.1 Plants life cycle

The life of a plant is like a cycle divided into two main phases: the **vegetative** and the **reproductive** phases. At the end of the latter, **seeds** (Box I.2) produced by the plant are dispersed and, if the environment is suitable, they germinate and establish as new individuals. These latter three stages – **dispersal**, **germination** and **establishment** (Box I.2) – are thus crucial but also limiting stages in the life of plants (Balcomb & Chapman 2003; Holl 1999; Stoner & Henry 2008).

Box I.2 Glossary

Fallback food: present year-round but incorporated into the diet when most preferred foods are scarce (Doran et al. 2002; Marshall et al. 2009; Marshall & Wrangham 2007); presumed to be vital to sustain consumer populations during periods of food scarcity (Brockman & van Schaik 2005).

Phenology: the study of seasonal cycles of biological phenomena *e.g.* the periodic flowering and fruiting of trees. (Forest Restoration Research Unit 2006; p.182)

Primate fruit: fruit syndrome defining fruits that are more attractive to primates as being large, large seeded fleshy fruits with an orange-brown coloration sometimes with husks, or harder coverings (Chapman & Russo 2007; Corlett 1998; Stoner & Henry 2008).

Seeds: considered according to their ecological sense, *i.e.* the hard bodies in the center of ripe fruits. Thus, true anatomical seed tissues may be excluded (*e.g.* arils), and fruit-derived tissues may be included (*e.g.* endocarps) in a seed. A seed defined in this way corresponds to the unit dispersed from the parent tree. (Lucas & Corlett 1998)

~~~

Seed dispersal: movement of seeds away from their parent plant (Nathan & Muller-Landau 2000);

Primary dispersal: movement of seeds away from their parent plant by the first dispersal agent (Chapman & Russo 2007);

Secondary dispersal: subsequent movement of seeds after they have been dispersed by primary dispersal (Wright et al. 2007).

~~~

Germination: splitting of the seed coat and spreading of the cotyledons (Wenny 2000). It consists of three overlapping processes. First of all, absorption of water causes swelling of the seed (**imbibition**) and splitting of the seed coat. Then, **food reserves** are mobilized (from the endosperm) and transported to the embryonic root (radicle) and shoot (plumule), which begin to grow and push against the seed coat. Finally, the radicle and plumule **emerge** through the seed coat (Forest Restoration Research Unit 2006).

Establishment: process during which a germinating seed takes root, uses up parental provisioning, and assumes independent growth as a seedling.

~~~

Autochory (*i.e.* dispersal by explosion);

Anemochory (*i.e.* dispersal by wind): seeds generally very small and light, often having structures (“wing”, “parachute” *etc.*) in order to limit their fall; fruits usually dry;

Barochory (*i.e.* dispersal by gravity);

Hydrochory (*i.e.* dispersal by water): used by plants located at the edge of water and producing seeds or fruits able to float;

Zoochory (*i.e.* dispersal by animals): seeds hold on to the animal (exozoochory; fruits usually dry), or are swallowed or stored in cheek pouches (endozoochory; fruits usually fleshy).
~~~

2.2.2 Multiple advantages for plants

Plants and animals depend on each other for the survival of their populations (Andresen 1999; Chapman & Chapman 1995). Frugivores benefit from this relation by winning food through the **sugar-rich flesh** of fruits and seed dispersal is an important process for plants **reproduction** (Andresen 1999). Indeed, thanks to the survival of a seed, the mother-plant, the population and finally the whole ecosystem can succeed. Several studies showed that the survival of fallen fruit is not sufficient to maintain populations of many tropical tree species (Chapman & Onderdonk 1998; Chapman et al. 1992). Thus, seed dispersal would be necessary to the survival of these populations and would determine their potential rates of recruitment, invasion, range expansion and gene flow (Nathan & Muller-Landau 2000).

But how can seed dispersal favour plants?

Escaping competition and predation

Many studies showed that seeds distribution follows a characteristic pattern. The curve describing the number of dispersed seeds according to the distance to the parent tree is **leptokurtic** (*i.e.* with a more acute peak around the mean and fatter tails). Basically, it means that most seeds fall directly under the parent tree. The remaining is dispersed away from the parent tree, with a progressive decrease (*i.e.* the tail) in seeds number as the distance to the parent tree increases (Willson & Traveset 2000).

The reduction in seeds number away from the parent tree is correlated with a reduction in their density. According to the **Janzen-Connell model** (Connell 1971; Janzen 1970), **non-dispersed seeds** – *i.e.* simply falling from the parent's canopy to the ground and facing a higher density – have a **lower probability of survival** (Bleher 2000; Chapman & Onderdonk 1998). This is due to **distance- and density-dependent effects**. First of all, competition for resources (water, nutrients) between seeds of the same tree is stronger if these seeds are close from each other (Gathua 2000; Howe & Smallwood 1982). Then, predators, pathogens, parasites, herbivores *etc*. strongly respond to a high seed density (Gathua 2000; Janzen 1970; Mangan et al. 2010) by concentrating their activities where resources are common. Seed dispersal may decrease this predation by limiting concentrations under parent trees (LoGiudice & Ostfeld 2002).

However, the density effect on the survival probability is not easily predictable. Actually, this effect seems to be highly **species-specific** (Chapman & Chapman 1995, 1996;

Chapman & Russo 2007; Lambert 2005; Lambert & Chapman 2005). This variability can be explained by the interaction of two factors. The proximity to the parent tree can imply a strong seed density and thus a **higher seed predation** (Connell 1971; Janzen 1970; Levin et al. 2003). But, it can also imply the presence of a very specific **microhabitat**, essential for seeds and seedlings' establishment (Levin et al. 2003). Depending on the particular rarity of this sort of microhabitat, seed dispersal can even occasionally be harmful for some seed species (Lambert 2001; Lapenta & Procópio-de-Oliveira 2008).

This "**escape hypothesis**" (Howe & Smallwood 1982) implies disproportionate success for seeds escaping the vicinity of the parent, as compared with those that fall nearby. Thus, even short dispersal distances can result in higher seedling survival (Clark & Clark 1984; Gathua 2000; Janzen 1970; LoGiudice & Ostfeld 2002).

Colonizing disturbances

Seed dispersal would promote the colonization of open habitats by helping pioneer species to invade degraded areas. This assumption is called the "**colonization hypothesis**" (Howe & Smallwood 1982).

Reaching suitable sites

Seed dispersal would increase the probability of **finding sites suitable for establishment** (Willson & Traveset 2000). This "**directed dispersal hypothesis**" (Howe & Smallwood 1982) implies adaptations ensuring seeds to reach this kind of sites (Gross-Camp & Kaplin 2005; Wenny 2001). Some species require definite conditions to germinate and establish. Seed dispersal can be a rewarding strategy by increasing the likelihood that at least some offspring reach the appropriate location (Willson & Traveset 2000). Several studies have highlighted this type of interactions. Wenny (2001) related the example of some ant species which take along seeds in their nest in order to consume their lipid-rich arils. Then, seeds can be abandoned in the nest where they benefit from a strong concentration in nutrients.

Avoiding inbreeding

The ecological and evolutionary **success** of any species ultimately depends on its ability to disperse and **spread its genes** (Pannell 2007; p.360). We know that seeds are better source of genetic diversity than pollen because they contain genes of both parents (against only one for pollen) (Forest Restoration Research Unit 2006). But, if a non-dispersed offspring reaches adulthood, the risk of future inbreeding is high (Willson & Traveset 2000). Seed dispersal is thus important to allow a correct genetic mixing between individuals of the same species (Forest Restoration Research Unit 2006) and to **avoid inbreeding**.

Increasing biodiversity

Seed dispersal determines the **spatial and genetic structure** of plant populations (Levin et al. 2003) but also increases the biodiversity within the ecosystem. According to the Janzen-Connell model (Connell 1971; Janzen 1970), only seeds dispersed at some distance from the nearest adult conspecific will survive. The space left available between the trees of this species will enable the establishment of another species (Wright & Duber 2001). Thus, the coexistence of several species and even the appearance of rare species can be observed (Howe 2000). This is the first step to the **biodiversity maintenance** or even **increase**.

The spatial distribution of individual plants mediates intra- and interspecific interactions, such as competition and density-dependent mortality, whose balance affects species coexistence (Chapman & Russo 2007). For example, limited seed dispersal of a better competitor may permits poorer competitors to establish to a particular site (Chapman & Russo 2007). Such limitations brought to a broader scale can contribute to the maintenance of the plant biodiversity (Palmer 1994; Wright 2002).

2.3 Prevalence and effectiveness of dispersers

2.3.1 Definition

Two factors import when defining the role played by seed-dispersing animal in plant regeneration (Andresen 2002):

¤ the **prevalence**, *i.e.* the number of species dispersed by the target disperser within the total number of species present in the plant community and

¤ the **effectiveness** (Schupp 1993) depending on:

- the **quantity** of dispersed seeds for each species, as well as
- the **quality** of this dispersal, *i.e.* the probability that a dispersed seed survives to produce a new reproductive adult

These two factors are complementary. Thus, an animal whose dispersal is prevalent but non effective will be of little interest in terms of forest regeneration. On the other hand, a species that is a very effective disperser for only a few plant species would be of great interest for these species but of limited interest for forest regeneration. The best would be to maintain healthy populations of animal species, both acting as prevalent and effective dispersers (Andresen 2002).

2.3.2 How to measure effectiveness?

Disperser effectiveness is ideally defined in terms of **'the contribution a disperser makes to the future reproduction of a plant'** (Schupp 1993). In order to measure it, the best would be to compare the number of new adult plants produced by the dispersal activity of an animal to the number produced by others. However, reliable estimates of these data can be very difficult to obtain. That is why measures based on seedlings, which may be nearly equivalent, are generally used.

The **quantity** depends on the **number of visits** made by a seed disperser at a feeding location. It will be influenced by several elements. First of all, the **abundance of seed dispersers** can strongly vary according to the site. Then, the **importance of fruits in the diet** and the **choice of individual fruits species** will induce differences in the number of visits. Finally, the **temporal and spatial reliability** of seed dispersers is also important. A reliable seed disperser visits plants throughout the days, the seasons and the years (this kind of temporal reliability is also called "predictability" (Balcomb & Chapman 2003)), and visit also all individuals of all populations throughout the range of the plant species (Schupp 1993).

The quantity also depends on the **number of seeds dispersed per visit** which is the product of the **number of seeds handled** by the **probability a handled seed is dispersed** (Valenta & Fedigan 2008). The quantity is thus strongly influenced by the length of a visit and by the handling method used by the animal (Schupp 1993). However, according to Schupp (1993), the number of visits made by a seed disperser would be a better predictor of the total quantity of seed dispersed than is the number of seeds dispersed per visit.

The **quality** of seed dispersal also depends on several elements. First of all, the **quality of the seed treatment in the gut** is evaluated from the **number of intact digested seeds** and the **germination percentage and latency** of these seeds. These figures generally vary according to the length of time seed spend in the gut (Schupp 1993; Traveset & Verdú 2002).

Then, the quality of seed dispersal depends on the **quality of seed deposition**, usually discussed in terms of the **probability a seed will be deposited in a suitable site** (Herrera & Jordano 1981; Schupp 1993). However, sites are not simply suitable or unsuitable. Indeed, the suitability of a site depends on the context: the life history stage (seed survival, germination and seedling growth and survival), the period, and the site (Schupp 2007). The seed disperser can make the distribution of seeds they disperse vary, so the disperser can also make vary the distribution of the survival probabilities created (Schupp 1993). Thus, the habitat selection, the rate and directionality of movements away from the fruiting tree, the rate and pattern of seed deposition, as well as the diet can strongly influence this element. In turn, each of these elements is influenced by the morphology, physiology, and behavior of the seed disperser, as well as the morphological and ecological characteristics of the dispersed species. In brief, suitable sites should provide (1) the stimuli necessary for breaking seed possible dormancy, (2) the conditions, such as light and temperature, required for germination to proceed, (3) the resources, such as oxygen and water, used in germination, and (4) the absence of hazards, such as seed consumers, competitors and pathogens.

3. Organization of the thesis

3. Organization of the thesis

3.1 Objectives of the study

This thesis relates the results obtained during the first long-term field study carried out on *Macaca leonina*. Contrary to a vast majority of studies, we decided to depict the overall plant-animal interaction process from both the animal and plant points of view. On the one hand, we studied the importance of macaques in seed dispersal and thus in forest regeneration. On the other hand, we studied the influence of resources and their availability on activities and movements of macaques. These two influences form a cycle and are completely dependent from each other.

3.2 Organization

This thesis consists of five chapters following the format of journal articles (Introduction – Methods – Results – Discussion – Literature cited) which can thus be read independently. The general conclusion allows connecting the discussions developed in each of the chapters. A final bibliography gathers all the references cited in the introduction and in the chapters.

The Chapter 1 "**Cercopithecinae as under-appreciated and over-persecuted gardeners in African and Asian disturbed habitats**" provides an outline of our current knowledge on seed dispersal by Cercopithecinae species and their specific role in forest regeneration. Also, this literature review shows how cercopithecines' tolerance to human disturbance may influence their importance as seed dispersers in degraded areas, and how much human-cercopithecines conflicts may be harmful for forest conservation. *The study is submitted to Conservation Biology.*

In the Chapter 2 "**Frugivory and seed dispersal by northern pigtailed macaques, *Macaca leonina*, in Thailand**", I analyze the effectiveness of northern pigtailed macaques as seed dispersers. I provide quantitative and qualitative data on pigtailed macaques' diet, seed processing, and dispersal. *The study is submitted to the Journal of Tropical Ecology.*

In the Chapter 3 "**Influence of wild and human food resources on ranging patterns of northern pigtailed macaques (*Macaca leonina*)**", I examine how a troop of pigtailed macaques may adapt its ranging behavior according to the spatiotemporal distribution of fruiting trees and may adapt its diet by including human food during fruit scarcity. *The study is submitted to the American Journal of Primatology.*

In the Chapter 4 "**Sleeping site selection and pre-sleep behavior in wild pigtailed macaques**", I investigate which pressure – predation and/or resources proximity – influences the physical characteristics and location of sleeping sites, trees, individuals' place in the tree, posture, and behavior of a troop of pigtailed macaques. *The study is published in American Journal of Primatology (2011) 73:1222-1230, DOI 10.1002/ajp.20993.*

The Chapter 5 "**The role of *Macaca* spp. in seed dispersal networks**", allows putting seed dispersal by pigtailed macaques back in a more biological context by exploring the specific and complementary seed dispersal services of *Macaca* species in relation to other seed dispersers usually encountered in a seed dispersal assemblage in the Indo-Malayan region. *The study is submitted to the Raffles Bulletin of Zoology.*

4. Study species: *Macaca leonina*

4. Study species: *Macaca leonina* (Blyth, 1863)

Considering the innumerable species registered in the IUCN red list (2011), it is unfortunately necessary to chose those which will become the focus of conservation efforts. Thus, when the overall goal is to maintain the regeneration ability of the tropical rainforest (Andresen 2002; Howe 1984), seed dispersers have to be protected. In this study we chose to focus on the **contribution of northern pigtailed macaques (*Macaca leonina*) in the regeneration of the tropical rainforest**. Indeed, few studies were carried out on this species, most of them being research notes (Davies 1990; Gippoliti 2001; Khamcha & Sukumal 2009) or only small parts of larger multi-species studies (Kitamura et al. 2002; MacKinnon & MacKinnon 1987; Suzuki et al. 2006; Whitington 1992) or evaluations of its conservation status (Choudhury 2003). Consequently, data concerning its ecology and behavior are highly limited (Choudhury 2008; Feeroz et al. 1994), making its study all the more important that today this species is considered vulnerable (IUCN 2011). The main threats are forest degradation – as, despite its high adaptability, *M. leonina* always need forest to survive –, hunting and capture from free-ranging populations to exploit them for picking coconuts (IUCN 2011; Sponsel et al. 2002). A better knowledge of *Macaca leonina* would allow a better protection since a degradation of its habitat will endanger this species, in the short term.

4.1 Description

4.1.1 Phylogeny and distribution

Order Primates
  Suborder Anthropoidea
    Infraorder Catarrhini
      Family Cercopithecidae
        Subfamily Cercopithecinae
          Genus *Macaca*

Northern pigtailed macaques belong to the family of Cercopithecidae and the subfamily of Cercopithecinae (Fooden 1975). Like other Old World monkeys, they are characterized by a relatively close-set, downward-pointing nostrils, ischial callosities and non-prehensile tail (Martin 1990).

Macaca is one of the most widespread genera of non-human primates. Indeed twenty-two species are found from North Africa to East Asia (Delson 1980; Fooden 1980; Thierry et al. 2004). Today, authors distribute them in at least three main species groups (Delson 1980; Fooden 1980): the *silenus* group (which *M. leonina* belongs to), the *fascicularis* group and the *sinica* group.

Macaca leonina is phylogenetically close to *M. nemestrina* but the former is distributed in Bangladesh, Cambodia, China, India, Lao People's Democratic Republic, Myanmar, Thailand and Viet Nam (Figure I.1), while the latter occurs in Peninsula Malaysia itself, and on the islands of Borneo and Sumatra (Caldecott 1986). Both, previously sub-species of *M. nemestrina,* were recently considered as two independent species (Gippoliti 2001).

Macaque diversity in Thailand (seven species: *M. fascicularis*, *M. mulatta*, *M. assamensis*, *M. arctoides*, *M. silenus, M. nemestrina* and *M. leonina*) is probably related to habitat diversity. Indeed, Thailand is an area of floral transition where deciduous forests are replaced by evergreen forests (Crockett & Wilson 1980).

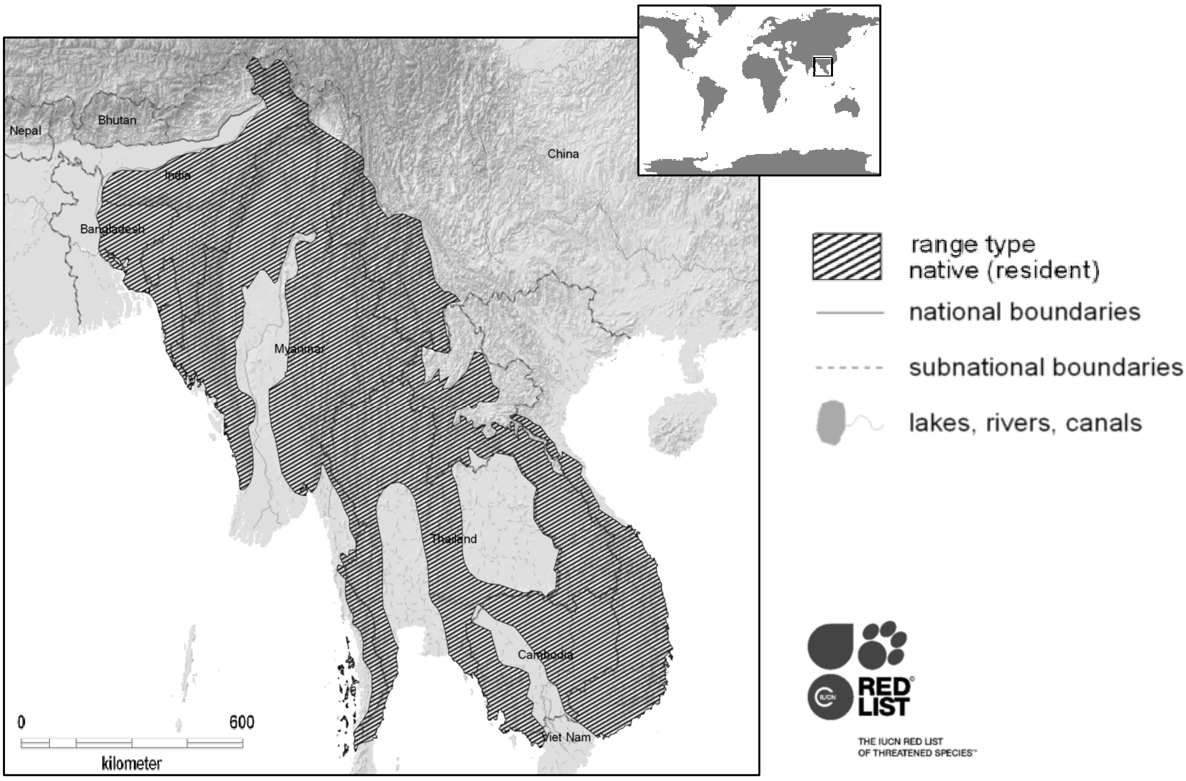


Figure I.1. Distribution of *Macaca leonina* (modified from IUCN 2011)

4.1.2 Social behavior

The social organization of northern pigtailed macaques is characterised by **multimale/multifemale** groups which consist of several adult males, a number of adult females, and their offspring (Melnick & Pearl 1987). Moreover, they show a high degree of sexual dimorphism (males range from 6.2 to 14.5 kg and females from 4.7 to 10.9 kg).

In most macaque species, the adult sex ratio is in favour of females (Ménard 2004). Indeed, *M. leonina,* seems to be characterized by a high number of females per male, with an average of more than four females per male (1:4.39) for one study troop (Albert, unpublished data). It is the same case for *M. nemestrina* (Oi 1990), *M. Silenus,* and *M. Arctoides* (Ménard 2004).

In every animal species, group size varies according to pressures depending on resource abundance and predation (Melnick & Pearl 1987). In pigtailed macaques, **semi-terrestriality** enables to exploit larger areas. This increases resources accessibility, and thus allows the survival of larger groups (Raemaekers & Chivers 1980). Thus, according to food availability, the group size of their closely related species, *M. nemestrina*, ranges from nine to 81 individuals (Oi 1990), which is comparable with other macaque species (Ménard 2004).

4.1.3 Diet

Macaques are the most **omnivorous** of **frugivorous** primates. According to the National Research Council of the National Academies (2003), their diet is composed of fruits, leaves, animals, bark, roots, pith, flowers and buds, mushrooms, and grass. However, they prefer to eat **fruits** when available (*e.g.* Hanya et al. 2003).

Macaca leonina mainly moves on the ground, which is known to decrease the costs of long-distance travels (Rodman 1979) and increases the variety of food sources by enabling foraging on invertebrates, ground vegetation, fungi, and fallen fruits (Caldecott et al. 1996) to which arboreal species do not have access. Pigtailed macaques thus have the possibility to forage in all levels of the rainforest canopy and on the ground which enables them to exploit climax evergreen forests as well as secondary forests and to survive in poor forests with scarce and scattered food resources.

4.1.4 Seed processing

Various fruit and seed processing techniques can be used by cercopithecines. They differ according to the primate and plant species (Chapman & Chapman 1996; Kaplin & Moermond 1998; Lambert & Garber 1998; Yumoto et al. 1998). Thus, a frugivore can alternate several seed processing behaviors depending on phenology patterns and resources' availability (Kaplin & Moermond 1998).

Cercopithecines mainly:

- **swallow**. The whole seed is swallowed, often with pulp. Then pulp is removed using the teeth and/or into the gut. Finally, the seed is defecated.
- **spit out**. The whole seed is put into the mouth and often into the cheek-pouches. Then pulp is removed using the teeth, and, finally, the seed is spat out.
- **drop**. The whole fruit is held in hands. Pulp and/or exocarpe are removed without entering the mouth. Then the seed (with or without pulp) is dropped.
- **destroy**. The seed is crunched and destroyed with the teeth. Then seed fragments are swallowed or spat out.

Thus cercopithecines can be (Kitamura et al. 2002):

- **seed dispersers** when dispersing intact seeds by either endo- or exozoochory.
- **neutral consumers** when leaving the seed intact under the parent tree.
- **seed predators** when destroying the seed.

4.2 Interest of pigtailed macaques

4.2.1 Why pigtailed macaques?

Several frugivore species coexisting with pigtailed macaques are known to be good seed dispersers. However, pigtailed macaques could be as good seed dispersers.

1) They eat **fruits in quantity**. This important frugivory implies the potential dispersal of many seeds (Latinne, unpublished data).
2) They eat a **high number of species**, more than other frugivores (Kitamura et al. 2002).
3) Like gibbons (McConkey 2000), their **gut** seems to **process seeds with care** (Latinne, unpublished data).
4) Their **cheek pouches** enable them to spit out seeds, which increases the number of techniques used to process seeds.

5) They have a **large home range** (Rowe & Myers 2011), larger than other species considered being good seed dispersers, such as gibbons (16 to 57 ha: Savini 2005).

More than being simple seed dispersers, northern pigtailed macaques could play an important role at various stages of succession during forest regeneration.

i) They seem to **cross various habitats** during the same day (Latinne, unpublished data).

ii) They are **semi-terrestrial** (Latinne, unpublished data). Their fast terrestrial movements can increase dispersal distances and enable them to cross deforested areas.

iii) They eat fruits of plant species belonging to **all plant life forms** present in the forest, from shrubs and lianas to tall trees. This diversity is probably due to the variability in fruit resources (Chapman & Russo 2007). According to Kitamura *et al.* (2002), macaques and bulbuls are the only seed dispersers consuming the fruits of arboreal shrubs. However, these shrubs play a central role at the beginning of succession because they enable the future establishment of sun-intolerant species, particularly thanks to a supply of shade and moisture on the floor.

iv) They belong to the **rare large frugivores** still present in Southeast Asia and potentially able to disperse large seeds. This is particularly relevant as many primary forest species are characterized by large seeds.

As suggested by some authors, pigtailed macaques could be one of the most important seed dispersal agents (Corlett 1998).

4.2.2 Pushed aside for bad reasons?

Cheek pouches would have a negative effect on seed dispersal

Macaques are pushed aside of dispersal studies for various reasons. First of all, they tend to store fruits in their cheek pouches and spit out many seeds, but some studies (Lambert 1999) showed that the majority of seeds were spat out under the parent tree. This induced the idea that macaques were not good seed dispersers. However, this technique could strongly benefit to several species. For some, it will reduce the probability of pathogen attacks by removing the pulp (Lambert 2001). For others, which require precise edaphic and ecological conditions, it will avoid the dispersal of seeds away from the microhabitat specifically adapted to their needs (Lambert 2001), which could not have been the case via fecal dispersal. Moreover, passage in the cheek pouches can improve seed germination. Yumoto *et al.* (1998)

showed that some plant species germination rates were significantly higher for seeds dispersed via the cheek pouches than for control seeds. Finally, seed spitting increases the diversity of techniques used by macaques to handle seeds (to swallow, to spit out, to drop) (Chapman & Russo 2007). When appearing within the same plant species, this diversity of handling techniques diversifies the dispersal conditions of this species, perhaps inducing an increase in its germination probabilities (Gross-Camp & Kaplin 2005; Kitamura et al. 2002).

Pigtailed macaques would be seed predators

During a long time, pigtailed macaques were considered as seed predators (Brockelman pers. com.). However, today we have reasons to think that the proportion of seed species destroyed by macaques is low (Latinne unpublished data).

The deposit would be inadequate

Sometimes, pigtailed macaques' feces contain a huge number of seeds, in particular when they ingest *Ficus* seeds. This clumped deposition can be harmful to species requiring some distance between seeds to ensure their survival and germination. These aggregations contrast with the dispersal carried out by small birds or bats which defecate in flight, thus scattering seeds over a wide area (Lucas & Corlett 1998).

Digestion would have a negative effect on seed dispersal

The retention time determines the abrasive effect on the seed-coat and germination success could decrease as retention time increases (Traveset & Verdú 2002). However, pigtailed macaques, like every cercopithecines, may have a long retention time.

4.2.3 An important but little known species

Actually, these received ideas come from **important gaps in our knowledge of this species**. Today, very little is known about pigtailed macaques in natural environments, their seed processing techniques and their role in seed dispersal. In fact, this lack of data even relates to the lack of studies on seed dispersal for many mammal groups in Paleotropics.

4.3 Study troop: base data

4.3.1 Habitat use

During our study, we collected base data on a troop of habituated northern pigtailed macaques living around human settlements. Within the troop home range, we distinguished two types of habitat: human settlements and forests. The "*human settlements*" habitat included tourist and associated buildings (staff housing, restaurants, bungalows), as well as the road crossing the tourist area, other housing, a section of the river and a small section of forest directly adjacent. The "*forests*" habitat refers to the continuous natural habitat and the river crossing the study area > 10 m away from the human settlements.

Studied pigtailed macaques displayed temporal variations in their habitat use over the study period. First, they spent more time near human settlements in the early morning and late afternoon, and more time in the forest in-between (Figure I.2). Second, they spent more time near human settlements during the dry season (November to April), and more time in the forest during the wet season (May to October) (Figure I.3).

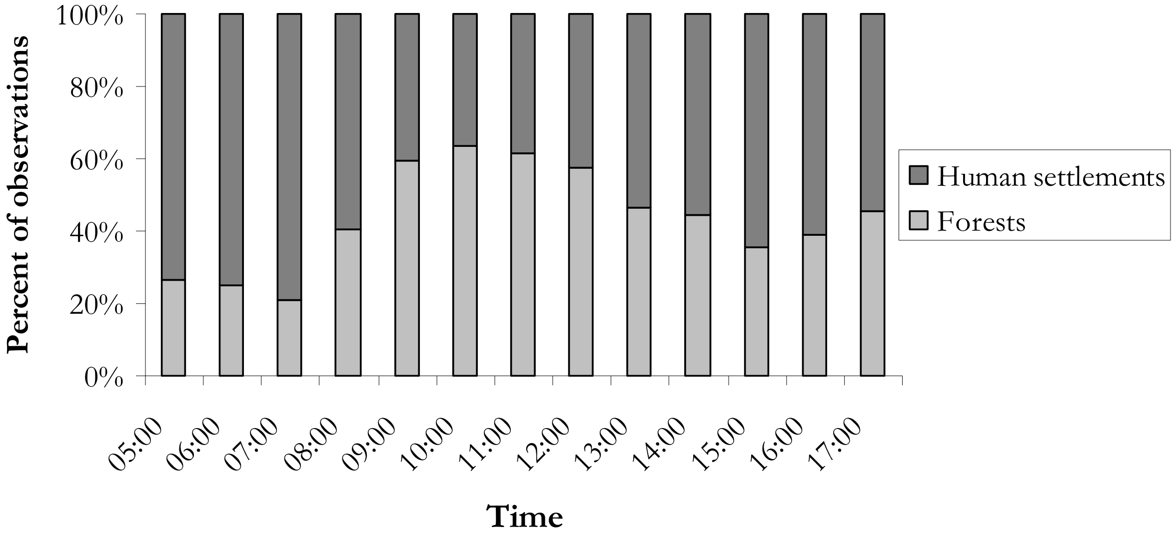


Figure I.2. Percentage of macaques' observations in each habitat (Human settlements and forests) according to day time. $N_{05:00}$=159 observations during scan sampling; $N_{06:00}$=1304; $N_{07:00}$=2002; $N_{08:00}$=1874; $N_{09:00}$=1784; $N_{10:00}$=1719; $N_{11:00}$=1658; $N_{12:00}$=1665; $N_{13:00}$=1638; $N_{14:00}$=1600; $N_{15:00}$=1697; $N_{16:00}$=1817; $N_{17:00}$=1960.

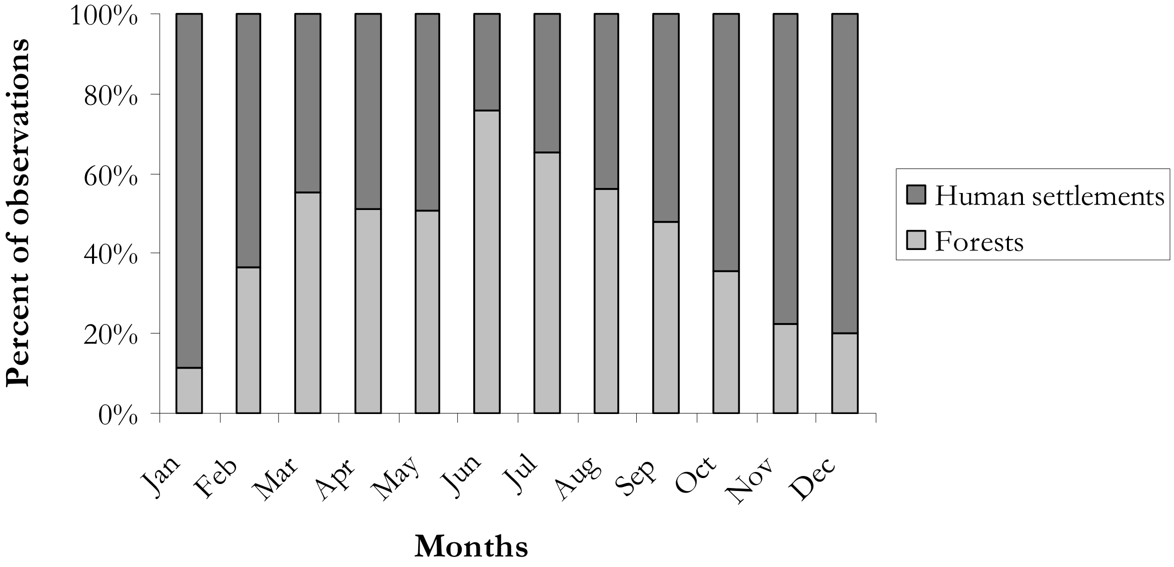


Figure I.3. Percentage of macaques' observations in each habitat (Human settlements and forests) according to months. N_{Jan}=1492 observations during scan sampling; N_{Feb}=2010; N_{Mar}=1781; N_{Apr}=1432; N_{May}=1876; N_{Jun}=1552; N_{Jul}=1426; N_{Aug}=1829; N_{Sep}=2031; N_{Oct}=1735; N_{Nov}=2041; N_{Dec}=1672.

4.3.2 Activity budget

The studied macaques also showed temporal variations in their activity budget. They were mainly moving or inactive during the early morning. Then, they showed a peak of social behaviors. After that, they foraged and ate while moving. In the late afternoon, they resumed social behaviors and inactivity (Figure I.4). Similarly, macaques' activity budget varied according to months (Figure I.5). There was a peak in movement in April. During the wet season, they continued to move a lot and, during the dry season, they moved and ate less and socialized more. Finally, macaques' activity budget varied according to age-sex classes (Figure I.6). The main difference lied in that young macaques moved more than adults.

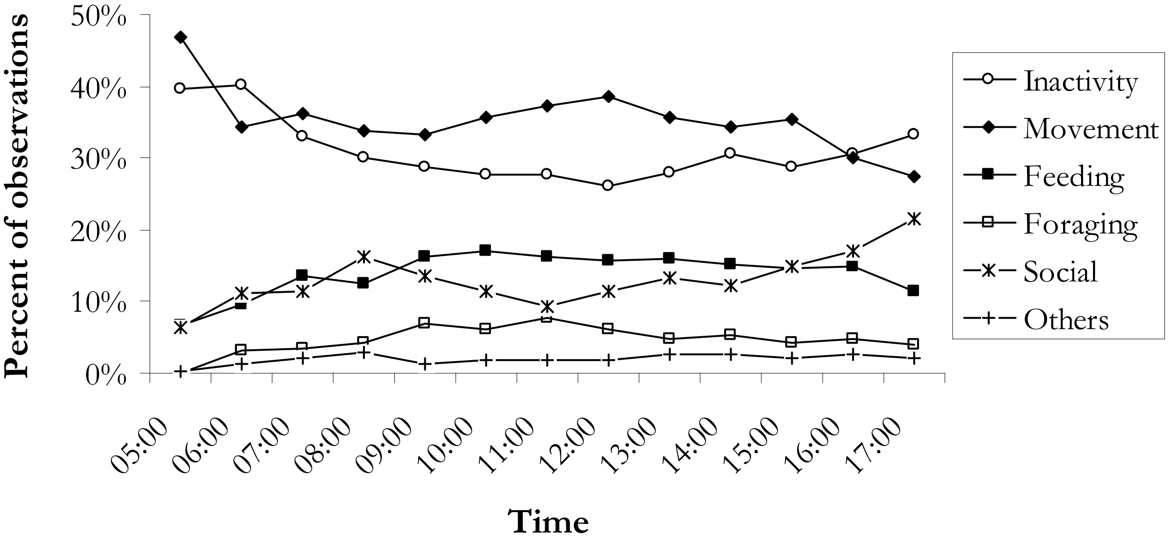


Figure I.4. Percentage of observations macaques were engaged in each activity according to day time. $N_{05:00}$=159 observations during scan sampling; $N_{06:00}$=1304; $N_{07:00}$=2002; $N_{08:00}$=1874; $N_{09:00}$=1784; $N_{10:00}$=1719; $N_{11:00}$=1658; $N_{12:00}$=1665; $N_{13:00}$=1638; $N_{14:00}$=1600; $N_{15:00}$=1697; $N_{16:00}$=1817; $N_{17:00}$=1960.

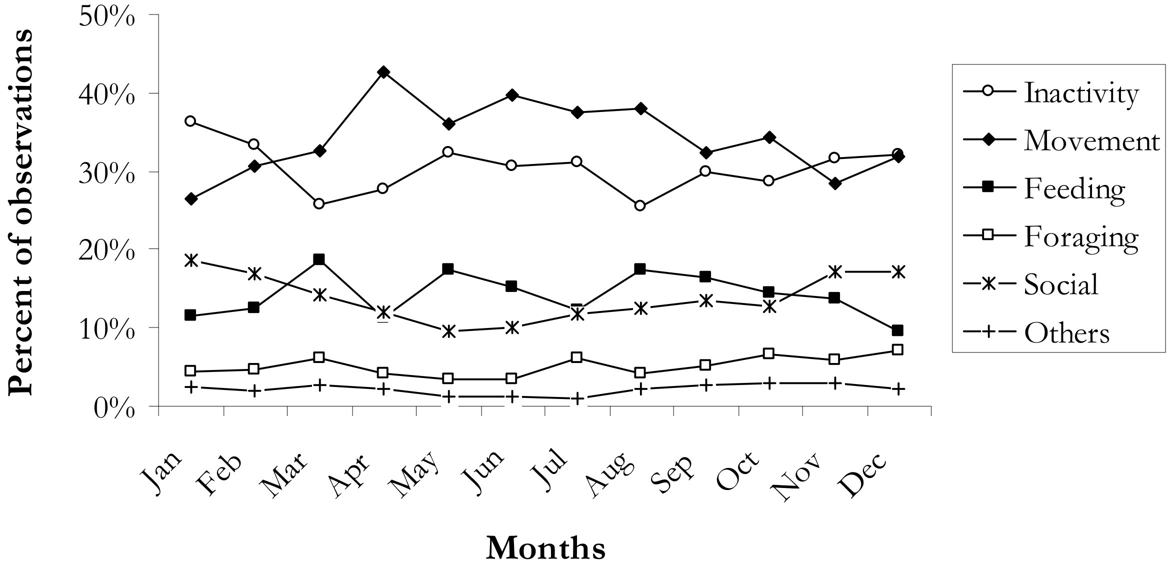


Figure I.5. Percentage of observations macaques were engaged in each activity according to months. N_{Jan}=1492 observations during scan sampling; N_{Feb}=2010; N_{Mar}=1781; N_{Apr}=1432; N_{May}=1876; N_{Jun}=1552; N_{Jul}=1426; N_{Aug}=1829; N_{Sep}=2031; N_{Oct}=1735; N_{Nov}=2041; N_{Dec}=1672.

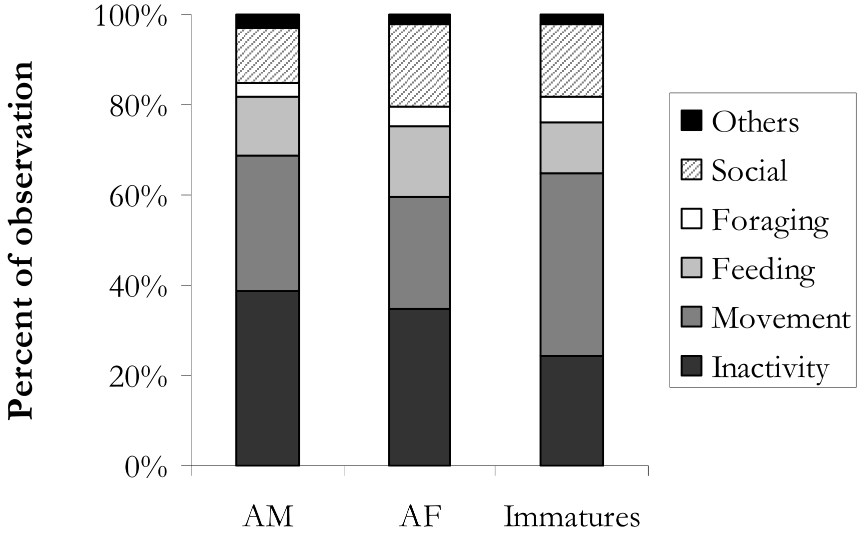


Figure I.6. Percentage of observations macaques were engaged in each activity according to age-sex class (AM: adult males; AF: adult females; Immatures: sub-adults, juveniles and infants). N_{AM}=2048; N_{AF}=8486; N_{Imm}=10,343

4.3.3 Diet

The studied macaques were omnivorous-frugivorous (Figure I.7) and often included human food in their diet (rice, fruits, bread, biscuits, etc.).

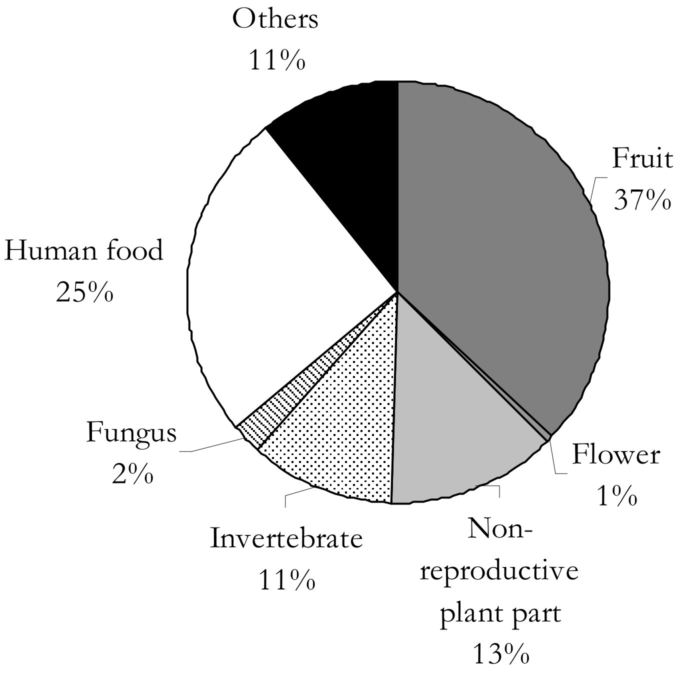


Figure I.7. Percentage of observations macaques were eating each item. N=1818.

The type of items consumed by macaques varied between habitats (Figure I.8). As expected, macaques ate more fruit in the forest, and human food and fruit in similar proportions near human settlements.

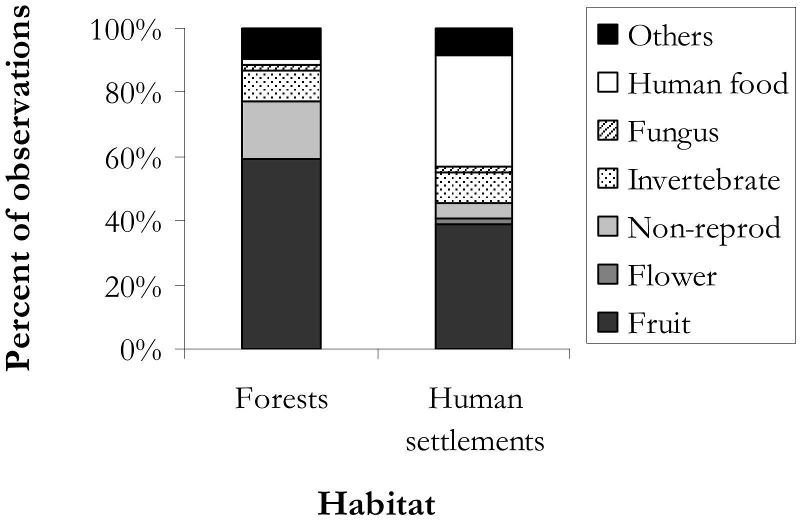


Figure I.8. Percentage of observations macaques were eating each item according to habitats (Forests and human settlements). N_{Forests}=725; N_{Hum}=1093.

5. Study site: Khao Yai National Park, Thailand

5. Study site: Khao Yai National Park, Thailand

5.1 Location

The study took place at the Khao Yai National Park (KYNP; 2,168 km²; 14° 05'–15'N, 101° 05'–50'E), in Thailand (Figure I.9). The study site is located around the park Visitor Center, an area of seasonally wet evergreen forest (Forest Restoration Research Unit 2000) at 700-800 m of elevation and including a ranger station and various tourist accommodations.

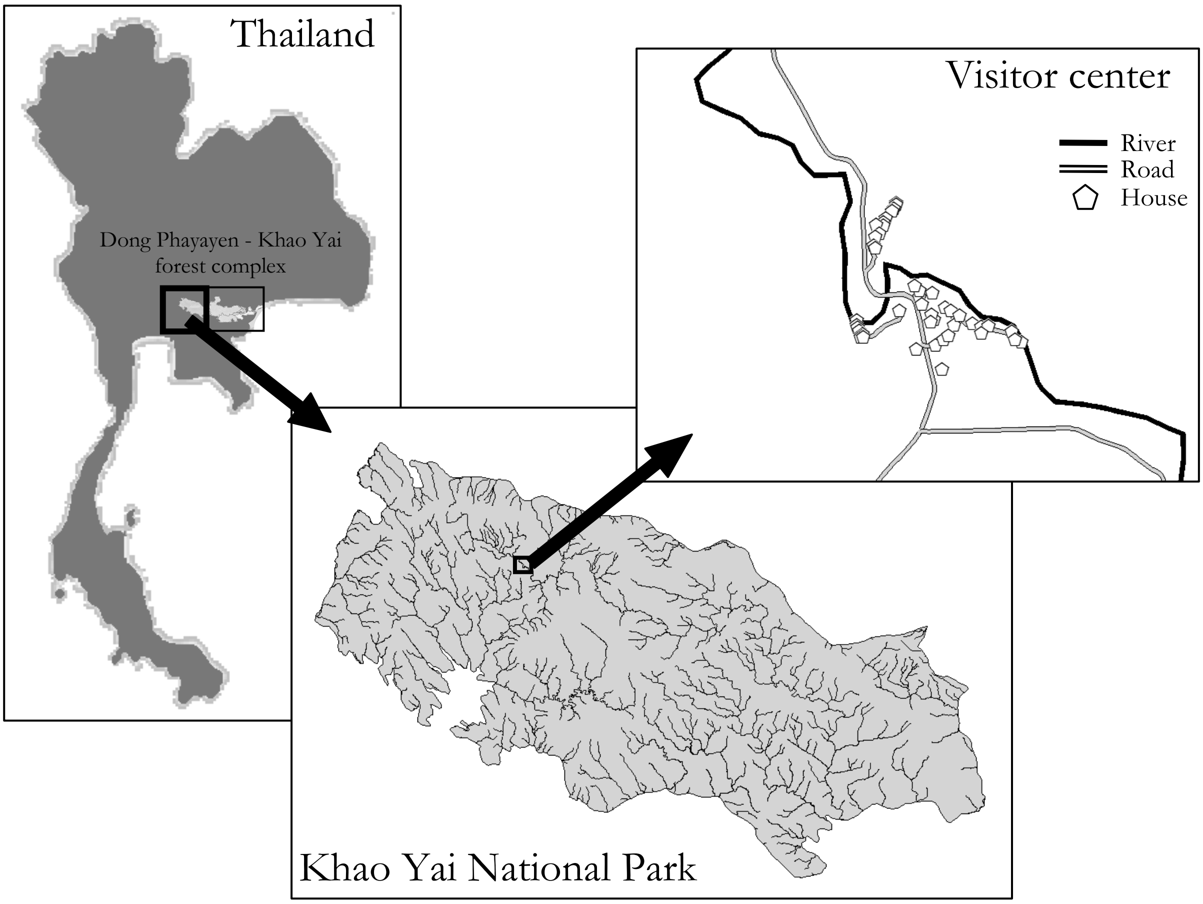


Figure I.9. Study site.

5.2 History

Around the 1950’s, before the park establishment, bandits took advantage of the isolation of mountains to settle and started to clear some forest fragments for cultivation. But in the early 1960’s, these people were evicted, leaving some patches of degraded forest, still recognizable in the current grasslands and secondary forests found around the Visitor Center.

When the KYNP, first park in Thailand, was established in 1962, Thailand's tropical forest had already suffered from a strong deforestation, due to the high population growth following the World War II. Today the KYNP is still the third largest park of Thailand and is part of the Dong Phayayen - Khao Yai (DPKY) forest complex, now a World Heritage Area, incorporating four National Parks and one Wildlife Sanctuary, and covering 6,199 km² (Figure I.9).

The park is relatively well protected now, but still suffers from poaching of the tree *Aquilaria crassna*, from which the resinous heartwood called agarwood is used as incense or for its essential oil in perfumery, and is still submitted to small-scale encroachments around its north-western and south-eastern margins (Lynam et al. 2006).

In 1996, a 30-ha Long Term Biodiversity Research Plot (Brockelman 1998) was established in the Mo Singto area, close to the park Visitor Center, to study gibbons' diet and foraging behavior in details. The plot is still used by researchers to study gibbons' and birds' ecology and forest dynamics.

5.3 Climate

The climate is monsoonal with a wet season (from May to October) and a relatively dry season divided into a cool (from November to February) and a hot (from March to April) period. The mean monthly temperature ranges from 19°C (December, January) to 24°C (March, April) and the annual precipitation averages 2,504 mm with monthly averages of 69 mm in the dry season and 353 mm in the wet season (2006-2010). Rainfall and temperature patterns were similar over the study years (2009-2010).

5.4 Flora

The KYNP is mainly covered by evergreen or semi evergreen forest, with small areas of mixed deciduous forest, scrubland and grassland (Lynam et al. 2006). Trees can reach 45 m in height (Kitamura et al. 2002) and the density of trees with a diameter at breast height (DBH) $\geq$ 10 cm is 490 ha^{-1} (Savini 2005).

Most phenological studies carried out in tropical rainforests seem to show a strong seasonality in fruits' availability which is often characterized by peaks of abundance and periods of scarcity (Raemakers et al. 1980 for Southeast Asia). The rainy season, due to high temperatures and, in particular, strong rainfalls, tends to favour fruit ripening (Corlett 1998). Thus, in Southeast Asia, fruit diversity and abundance are relatively high during the rainy season and reach a low point at the beginning of the dry season (Kitamura et al. 2008). This seasonal variation influences strongly the frugivores' community which faces irregularities in its food resources.

5.5 Fauna

The KYNP hosts 46 mammal species, including four primate species: the white-handed gibbon (*Hylobates lar*), the pileated gibbon (*Hylobates pileatus*), the slow loris (*Nycticebus coucang*), and the pigtailed macaque (*Macaca leonina*). Macaques and gibbons are known to be feeding competitors (Whitington 1992). It also contains 358 bird species and 63 reptile species.

Both birds and mammals include macaques feeding competitors – the great hornbill (*Bucero bicornis*),the wreathed hornbill (*Aceros undulatus*), the oriental pied hornbill (*Anthracoceros albirostris*), the brown hornbill (*Anorrhinus tickelli*), the Asiatic black bear (*Ursus thibetanus*), and the Malayan sun bear (*Ursus malayanus*) – but also potential predators – the clouded leopard (*Neofelis nebulosa*), the Asian golden cat (*Felis temminckii*), the mountain hawk eagle (*Spizaetus nipalensis*), and the crested serpent eagles (*Spilornis cheela*).

CHAPTER 1

Cercopithecinae as under-appreciated and over-persecuted gardeners in African and Asian disturbed habitats

© Hans Hillewaert © Daniel Wambach © Amy Jackson © Julie Platel

Albert, A., McConkey, K., Savini, T., Huynen, M.-C. Cercopithecinae as under-appreciated and over-persecuted gardeners in African and Asian disturbed habitats. Submitted to Conservation Biology.

Résumé

La déforestation provoque un déclin mondial dans l'abondance des populations de frugivores et réduit la biodiversité des forêts tropicales. Les espèces végétales à large graines, provenant des forêts primaires, sont menacées car elles dépendent d'un nombre restreint de grands disperseurs, eux-mêmes vulnérables car sujets à une chasse sélective et à la dégradation de leur habitat. Parmi ces disperseurs, certaines espèces sont plus tolérantes que d'autres face aux dégradations induites par l'Homme. Les cercopithécines sont particulièrement résistants étant donné leur semi-terrestrialité et leur régime omnivore. Cependant, cette tolérance aux hommes pourrait être, à long terme, la raison principale de leur disparition. L'augmentation croissante de la population humaine provoque une compétition directe entre l'Homme et les populations d'animaux sauvages, augmentant d'autant la fréquence des conflits Homme-vie sauvage. La perception négative des cercopithécines par les populations locales est une menace majeure pour leur conservation. Ceci est d'autant plus alarmant que les cercopithécines sont parmi les seuls disperseurs efficaces pour les espèces à large graines dans les habitats dégradés d'Asie et d'Afrique. En effet, les cercopithécines manipulent les graines de différentes manières et peuvent ainsi déféquer, déposer ou stocker les graines dans leurs poches jugales. L'utilisation de ces-dernières permet aux macaques de manipuler de larges graines à mesure qu'ils se déplacent. Cette caractéristique, combinée avec de larges domaines vitaux et des groupes généralement grands, résulte en la dispersion de beaucoup de graines loin de leurs arbres parents, c'est-à-dire là où la probabilité de survie de ces graines est plus importante. La conservation des cercopithécines pourrait donc être primordiale pour la régénération des forêts dégradées, rendant essentiel la compréhension des causes de conflits Homme-cercopithécines afin d'enrayer le déclin des populations de Cercopithecinae.

***Mots-clés* :** primates ; fragmentation ; dispersion des graines ; régénération de la forêt ; Asie ; Afrique.

Abstract

Deforestation induces a global decline in the population abundance of frugivores and reduces tropical forest biodiversity. Large-seeded plant species from primary forests are threatened by disturbance as they depend on a restricted number of large-bodied dispersers that are vulnerable to extinction through selective hunting and habitat degradation. Among these dispersers, some species are more tolerant to human disturbance than others. Cercopithecines are particularly resilient to disturbance because of their semi-terrestrial habits and omnivorous tendencies. However, this tolerance to human disturbance could be, in the long term, the very reason for their disappearance. Escalating human population growth brings human and wildlife populations into direct competition, increasing the occurrence of human-wildlife conflicts. The negative perception of cercopithecines by local people poses a major threat to their conservation. This is a cause of concern because cercopithecines are among the only effective dispersers of large seeds in Asian and African disturbed habitats. Cercopithecines handle fruits in multiple ways, and may swallow, drop or store seeds in their cheek pouches. Cheek-pouch use allows the monkeys to process large seeds as they move; this characteristic combined with large home ranges and frequently large groups results in many seeds being scattered away from parent trees, where the probability of seed survival is higher. The conservation of cercopithecines could be significant for the regeneration of degraded forests. It is essential that the causes of human-cercopithecine conflicts are understood to mitigate declines in Cercopithecinae populations.

***Key words*:** primates; fragmentation; seed dispersal; forest regeneration; Asia; Africa.

Introduction

Habitat disturbance and hunting

Global deforestation rates have been increasing over the last decades (Pereira et al. 2010). This results mainly from the increased exploitation of natural resources, such as palm oil, timber or firewood, following human population growth (Butler & Laurance 2008; Cowlishaw & Dunbar 2000; Wright & Muller-Landau 2006). The disturbed habitats that are created (*i.e.* fragmented, logged or cleared areas) are characterized by the loss of many animal and plant species (Brook et al. 2003), directly from their habitat limitation, and indirectly from the loss of inter-specific interactions necessary to the ecosystem survival (Dunn et al. 2009; Wright & Muller-Landau 2006). The deforested areas are frequently converted to plantations, pastures, or even urbanized areas where few animals can thrive (Cowlishaw & Dunbar 2000), and even these animals are often threatened by hunting (Corlett 2007; Laurance et al. 2006).

The disappearance of seed dispersers

The global decline in frugivore diversity and population abundance has consequences for forest maintenance, regeneration and, in the long term, biodiversity (Dirzo 2001). Forest disturbance and hunting remove seed dispersers and predators (Corlett 2007; Kirika et al. 2008; Wright et al. 2007). On the one hand, the abundance of some plant species is reduced, due to a lack of seed dispersers (Chapman & Chapman 1995; Muller-Landau 2007). On the other hand, the density regulation of already common species is limited, because of a lack of seed predators (Muller-Landau 2007; Wright et al. 2000).

Functional replacement of a lost frugivore may be possible (Howe 1984) but has not yet been documented. Redundancy in the seed dispersal role of a frugivore is less likely for especially effective dispersers (Brodie et al. 2009; Jordano et al. 2007; McConkey & Brockelman 2011) and those that are able to disperse large seeds. Indeed, the dietary overlap between large frugivores, especially birds and mammals, tends to be low (Donatti et al. 2011; Savini & Kanwatanakid-Savini 2011). Even a reduction in frugivore population abundance can have the same effect as its local extinction, if the decline prevents that species from providing its services at the required levels (Cowlishaw & Dunbar 2000; McConkey & Drake 2006; Redford & Feinsinger 2001).

The last big seed dispersers

Seed dispersal becomes especially critical for forest regeneration as land degradation becomes more severe and less floristic resources are available (da Silva et al. 1996; Duncan & Chapman 2002). This problem results mainly from the low number of animal-dispersed seeds that are brought into disturbed areas (Duncan & Chapman 1999; Vulinec et al. 2006) exerting low attraction on potential dispersers by their low fruit abundance (da Silva et al. 1996) and high predation risk (Duncan & Chapman 2002). Many studies highlight the seed dispersal role of birds and bats in disturbed habitats (Medellin & Gaona 1999; Muscarella & Fleming 2007). Seed dispersal by primates might also be important for restoration (Lambert & Chapman 2005) but remains understudied, given the abundance of primates in tropical forests (25-40% of the frugivore biomass; Chapman 1995). Primates are particularly important in the dispersal of mid- and late- successional species (Duncan & Chapman 2002; Kaplin & Lambert 2002). These species are often characterized by large seeds (> 10 mm) (Kaplin & Lambert 2002) which can only be ingested by a few species of large frugivores (Chapman et al. 2009; Cramer et al. 2007; Kitamura et al. 2002), vulnerable to extinction due to selective hunting (Chapman et al. 2009; Vanthomme et al. 2010) and habitat loss or degradation (Corlett 1998; Johns & Skorupa 1987; Kitamura et al. 2002). Thus, in forest fragments where seed dispersers' populations have been reduced, an increase in the proportion of small-seeded species has been documented (Chapman & Onderdonk 1998; Cramer et al. 2007). Today, the restoration of Asian and African forests in critical situations could come from Cercopithecinae (Gray, 1821), which are often highly frugivorous, effective dispersers and, interestingly, surviving in human-disturbed areas.

The aim in this review was to evaluate the potential importance of Cercopithecinae as seed dispersers in disturbed habitats, by summarizing the literature on their tolerance to disturbance and their role in seed dispersal. We determined which cercopithecine characteristics enhance their tolerance to habitat disturbance, reviewed the literature on their seed dispersal role and assess how this role can be beneficial for the maintenance or recovery of forest-dependent plant species in degraded areas.

Methods

We searched the available literature for studies on cercopithecine seed dispersal, habitat tolerance and threats. Tolerance to disturbance was classified as follow: (1) highly tolerant species (T+) are able to survive in highly disturbed habitats (*e.g.* urban areas); (2) tolerant species (T-) are able to survive in disturbed habitats (*e.g.* rural areas, plantations, young secondary forests, fragments); (3) intolerant species were know to be intolerant to habitat disturbance.

Variations between cercopithecine species according to habitat-occupied, locomotion mode, diet and intensity of cheek pouch use could explain their tolerance to disturbance. To assess the relative importance of each factor in determining the tolerance of cercopithecine species we used a multivariate analysis. We used the program Statistica 10.0 to perform a Multiple Correspondence Analysis (MCA) on the 52 species for which we had complete data. Factors included in the MCA were habitat (Forest, Forest+Non-forest, Non-forest), locomotion mode (Terrestrial, Semi-terrestrial, Arboreal), diet (Omnivorous, Omnivorous-Frugivorous, Omnivorous-Other, Other diet), intensity of cheek pouch use (Low, Medium, High), and tolerance to disturbance (Low, Medium, High) of each cercopithecine species.

Cercopithecinae

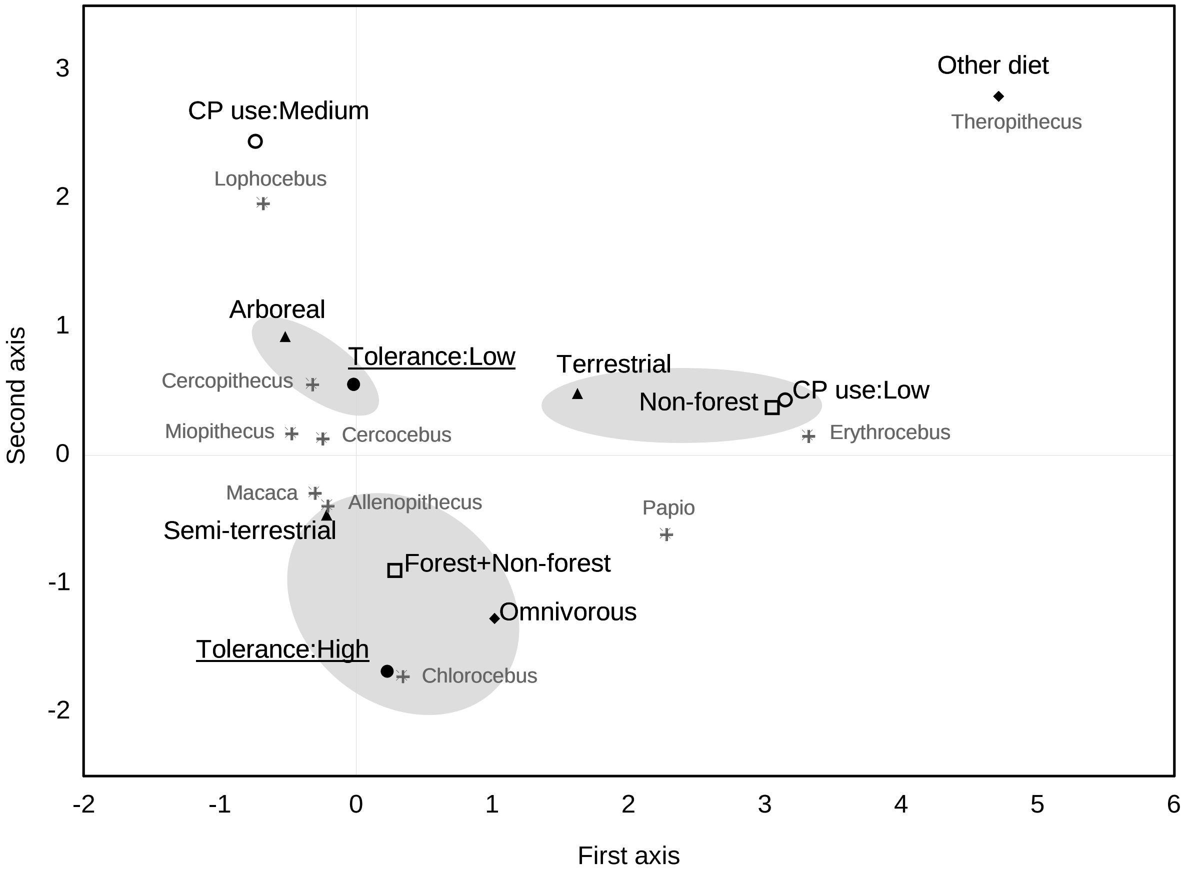
Range and habitats

The family Cercopithecinae includes 12 genera and 67 species (Wilson & Reeder 2005) (Appendix 1.1). Eleven of these genera are distributed in sub-Saharan Africa. The remaining genus, *Macaca*, is one of the most widespread non-human primate genera, with 22 species (33% of all cercopithecine species) ranging from North Africa to East Asia. Cercopithecinae species are adapted to a range of habitats. Most species (94%) have all or some populations inhabiting forests, with the remaining species found in non-forest habitats (Appendix). All Cercopithecinae species live within the tropics (Oates 1987), except two species (*Macaca fuscata* and *M. sylvanus*) which are adapted to temperate areas.

Human-disturbance tolerance

Contrary to the vulnerability their large body size and mainly frugivorous diet suggest (Johns & Skorupa 1987), 57% of cercopithecine species are tolerant to human disturbance and only 21% are intolerant (tolerance of the remaining 22% is not known) (Appendix 1.1). Some species even seek human presence for the advantages it provides (*i.e.* weed species; Richard et al. 1989) with nine species (13%) able to persist in urban environments. The MCA ordination mainly related tolerance level to habitat, diet and locomotion mode (Figure 1.1). The first MCA axis accounted for 59% of the variance and separated species according to diet, cheek pouch use and habitat. The second axis represented 23% of the variance, and separated species according to tolerance level and diet. The MCA ordination enabled us to distinguish three clusters: (1) arboreal species with low tolerance to disturbance; (2) terrestrial species living in non-forest habitats and using their cheek pouches infrequently; and (3) omnivorous, semi-terrestrial species, living in forest and non-forest habitats and showing a high tolerance to disturbance. These results show that the high tolerance of some cercopithecines species could be due to their high flexibility and adaptability (Hill 2000; Johns & Skorupa 1987) – behavioral (traveling on the ground as well as in the trees) as well as dietary (omnivorous). Thus, they can adapt their home range size and location as well as their diet to habitat disturbance (Tutin et al. 1997b; Twinomugisha et al. 2006), such as forest clearing for agriculture (Riley 2007), or even exploit human activities (Boulton et al. 1996; Ram et al. 2003). On the contrary, forest dependent species, due to their arboreal habits or their reliance on more specific dietary items are less likely to be tolerant to forest disturbance.

Figure 1.1. Trait values and inter-trait distances for the first two axes obtained in the Multiple Correspondence Analysis. Gray ellipses indicate clusters of traits discussed in the text. Only traits accounting for more than the mean variance of the axis are shown on the graph. Habitats: Forest+Non-forest, Non-forest; locomotion mode: Terrestrial, Semi-terrestrial, Arboreal; diet: Omnivorous; intensity of cheek pouch use: Low; level of tolerance to disturbance: Low, High. Genera are also shown for information.



Conflict with humans

Disturbance tolerance favors the survival of cercopithecines but could also cause, in the long term, their disappearance. Human population growth brings human and wildlife into direct competition within an increasingly overlapping niche (Priston 2005; Sillero-Zubiri & Switzer 2001). Most cercopithecine genera have populations that raid crops and come into conflict with farmers – *Papio* (Weyher et al. 2006), *Macaca* (Priston 2005), *Cercopithecus* (Naughton-Treves 1998), *Chlorocebus* (Saj et al. 2001), *Mandrillus (IUCN 2011), Theropithecus* (Lee & Priston 2005), *Erythrocebus* (Lee & Priston 2005) and *Cercocebus* (Wieczkowski 2005). Indeed their intelligence, their ability to travel quickly on the ground (79% of species are terrestrial or semi-terrestrial) and their cheek pouch use (enabling them to store more food) make them successful crop-raiders (Warren 2008). Agonistic interactions between cercopithecines and humans in cities (Chauhan & Pirta 2010) frequently lead to a negative perception of the monkeys by local people, which also poses a major threat to their conservation (Hill & Webber 2010; Lee & Priston 2005). The lethal control of “pests” has caused the extinction of several animal species (Woodroffe et al. 2005) and cercopithecines could undergo the same fate since macaques, baboons and vervet monkeys are sometimes killed in retaliation for raiding (Boulton et al. 1996; IUCN 2011; Priston 2005; Strum 2010).

Seed dispersal by Cercopithecinae

The disturbance tolerance of cercopithecines could be essential for the regeneration of degraded areas as they can contribute to seed dispersal in disturbed areas or between fragments. Moreover, even some species, seemingly dependent on intact forests, regularly cross gaps, or feed in the non-forest matrix (*e.g.* when they raid crops) and are potentially important seed dispersers across gaps and intro degraded areas.

All cercopithecine species are omnivorous (with the exception of *Theropithecus gelada*) (Appendix 1.1) and 70% are partially frugivorous. Cercopithecines are unique among primates because they disperse seeds in three different ways (Yumoto et al. 1998): epizoochory (dispersal via the outside of the animal, *e.g.* by dropping), endozoochory (dispersal via feces, *i.e.* by swallowing) and synzoochory (dispersal by storing fruit in cheek pouches and spitting seeds out). They alternate these seed processing techniques according to phenology patterns, plant species and resource availability (Kaplin & Moermond 1998; Tsujino & Yumoto 2009) and may even use various deposition patterns for the same plant species. This creates a unique seed shadow and can increase the species’ germination probability (Gross-Camp & Kaplin 2005; Schupp et al. 2010). Cercopithecines may also be seed predators for certain species (Dominy & Duncan 2005; Wrangham et al. 1998; Chapter 2).

Spitting-out

Cheek pouches – oral, bilateral sacculations formed in the inferior mouth part (Murray 1975) – are a major characteristic of cercopithecines. They are used by animals mainly to store fruits while continuing to move, which has beneficial consequences for seed dispersal (Lambert 2005). The whole fruit is taken into the mouth and may be stored in the cheek pouches. Fruits are then returned one by one to the oral cavity where pulp is removed and the seed is spat out. This process avoids carrying inert seed bulk in the gut (Lambert 1999) and increases the nutrient gain though a more efficient flesh mastication (Corlett & Lucas 1990).The variability in size and position of cheek pouches among the different genera matches the variability in the documented use of the cheek pouches (Murray 1975) (Appendix 1.1). Most species (72%) have large cheek pouches they use frequently, while the six species with small cheek pouches use them infrequently.

This unique mode of seed dispersal has several benefits to seed dispersal, and, potentially, to restoration of degraded areas. Although seed-spitting has frequently been associated with high proportions of seeds spat under parent trees (Lambert 1999; Lambert 2001), high removal rates have been documented for some plant species (McConkey et al. unpublished data) and it can be an effective form of dispersal (McConkey & Brockelman 2011). Spat seeds are frequently scattered singly over the forest floor as the monkey travels from the food source, at recorded distances exceeding 100 m (Tsujino & Yumoto 2009). These seeds may have a lower risk of attack by density-dependent predators and higher germination compared to clumped seeds. Pulp removal is also advantageous for the seed because pulp often contains germination inhibitors (Cipollini & Levey 1997; Traveset 1998), and this action would be beneficial in areas where alternative dispersers are not available.

Cheek-pouch use also allows cercopithecines to disperse large-seeded species, since they are limited by cheek-pouch size (not by what they can swallow) and can potentially disperse larger seeds than seed-swallowing primates (*e.g.* 25 mm in *Cercopithecus lhoesti* vs 15 mm in *Pan troglodytes schweinfurthii*; Gross-Camp & Kaplin 2011). Finally, when cercopithecines do not swallow seeds, which would be inert bulk in their gut, they can probably consume many more seeds than seed swallowing primates (Corlett & Lucas 1990; Lambert 1999; McConkey & Brockelman 2011).

Swallowing

Seed swallowing – and subsequent deposition in the feces – is the most commonly reported seed handling behavior in primates and generally results in the longest dispersal distances (Chapman & Russo 2007). Cercopithecines vary among and within species in the maximum seed sizes they swallow (4 mm in *Macaca fascicularis* (Lucas & Corlett 1998); 20 mm in *Macaca leonina* (Chapter 2); 30 mm in *Cercopithecus nictitans* (Chapman et al. 2009); 42 mm in *Mandrillus leucophaeus* (Astaras & Waltert 2010)) but swallowed seeds tend to be smaller than spat seeds (Lambert 1999; Lucas & Corlett 1998).

Seed swallowing has two potential benefits to seed dispersal. First, defecated seeds are retained longer than spat or dropped seeds, resulting in longer dispersal distances. Cercopithecines have among the longest gut retention times across the primate order (*e.g.* 25.8 hours in *Papio anubis*, 19.7 hours in *Cercopithecus ascanius*, 31.5 hours in *Cercopithecus aethiops*; Lambert 1998; Lambert 2002), contrary to most frugivorous primates whose gut passage times are typically in the range of a few hours (Setchell & Curtis 2003). As cercopithecines can cover relatively long distances daily (200 to 13,000 m/day, with most populations traveling more than 1000 m/day) (Appendix 1.1), they are potentially long distance dispersers. When combined with a tolerance to disturbance, they can disperse seeds between forest fragments (Duncan & Chapman 2002).

Seed swallowing also affects germination because of mechanical or chemical scarification of the seed coat (Traveset & Verdú 2002), removal of the pulp which reduces pathogen attack and removes germination inhibitors (Lambert 2001; Pringle et al. 2007), and the presence of fecal material which may influence germination and/or future seedling growth. The few studies that have been conducted on cercopithecines, however, have found positive, neutral or negative gut passage effects, dependent on plant species (Otani 2004).

The clumped seed deposition resulting from defecation can be harmful to species requiring distance between seeds to ensure their survival (Janzen 1970; Kwit et al. 2004), and cercopithecines are probably poor dispersers of especially small seeds (*e.g. Ficus* species) because they are frequently deposited on the ground in clumps containing 1000's of seeds (Chapter 2). This contrasts with dispersal by small birds or bats which defecate in flight and scatter seeds over a wide area (Lucas & Corlett 1998). The disadvantage of a clumped deposition, however, is alleviated by secondary dispersers such as dung beetles (Andresen &

Levey 2004; Culot et al. 2009), ants (Levey & Byrne 1993) and scatter-hoarding rodents (Li & Zhang 2007), which scatter the seeds and may deposit them in a suitable site.

Dropping

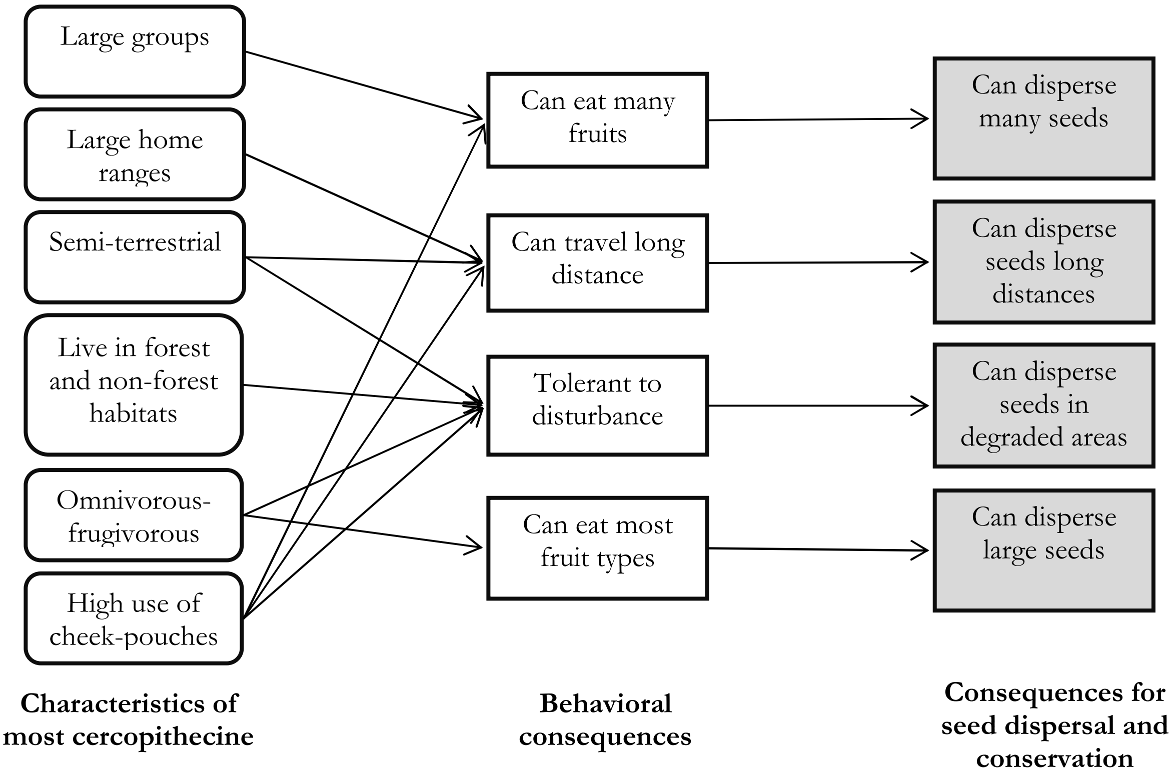
The largest fruits processed by cercopithecines are transported in the hands. The seeds are cleaned at the front of the mouth and then the seed is dropped. Most seeds are dropped at short distances from the parent plant, but longer distances have been recorded (*e.g.* 130 m for a *Mangifera indica* seed by *Macaca leonina*; Chapter 2). Although this is an inefficient form of dispersal, it may be the only dispersal means for some large-seeded species in degraded areas where large dispersers are absent (Nakashima et al. 2008) and it also benefits the seed through the removal of the pulp and/or exocarp, which reduces pathogen attack (Lambert 2001).

Influence of Cercopithecinae eco-ethological characteristics on seed dispersal

The dispersers' behavior during feeding and seed processing directly influences the spatial distribution of a plant's seeds (*i.e.* seed shadow; Nathan & Muller-Landau 2000). Consequently, variability in diet, movement patterns and morphological characteristics (*e.g.*, cheek-pouch size and use) amongst cercopithecines influences their seed dispersal effectiveness and potential importance in degraded areas (Figure 1.2).

Retention time of seeds (and, therefore, dispersal distance) is determined by a combination of factors, including diet composition, morphological and physiological characteristics of the animal (*e.g.* body size, gut size and anatomical specializations; Lambert 1998; Traveset 1998), as well as seed size, weight and volume (Cipollini & Levey 1997; Lambert 1998; Willson & Traveset 2000). Most cercopithecines are frugivorous but also consume leaves, invertebrates and vertebrates, and in anthropogenic areas, human food (Brotcorne et al. 2011; Ram et al. 2003). This generalist diet suggests cercopithecines can survive in disturbed habitats offering few fruit resources and also means they consume fruit from a large range of plant taxa (*e.g.* 185 fruit species in *Macaca fascicularis* for a 17-month period (Lucas & Corlett 1998), 110 in *Mandrillus leucophaeus* for a 12-month period (Astaras & Waltert 2010), 79 in *Papio anubis* for a 24-month period (Kunz & Linsenmair 2008)).

Figure 1.2. Influence of eco-ethological characteristics of most cercopithecines on seed dispersal and forest regeneration.



In heterogeneous habitats the resources are scattered (Oates 1987), and cercopithecines are well-adapted to exploiting a patchy resource distribution. Because they are forced to travel between food patches the probability of dispersing seeds far from the parent tree are higher (Lambert 2005), and their disturbance tolerance makes them likely to disperse seeds in degraded areas (and between fragments) and to help forest regeneration (Corlett 1998).

Most cercopithecines travel long distances daily (Appendix 1.1), suggesting potential seed dispersal distance may exceed one kilometer, although actual distances will be limited by home range size, and this is variable between species (Appendix 1.1). Macaques, patas monkeys, mangabeys and baboons exploit large home ranges and can disperse seeds farther than guenons or geladas exploiting smaller home ranges (Murray 1975). During a given period, macaques travel mainly between high concentrations of a given fruiting plant species.

This results in the dispersal of seeds within the specifically suitable habitat in which the conspecific adult trees are distributed, which may increase the seed survival probability (Tsujino & Yumoto 2009).

The Cercopithecinae various locomotion modes also influence seed shadows. Terrestrial or semi-terrestrial species tend to travel faster than arboreal ones (Rodman 1979). The formers, with their usually large home range (Appendix 1.1), may therefore move seeds farther from the parent tree.

More frequent use of cheek pouches could result in more efficient seed dispersal, because more seeds can be processed, larger seeds can be dispersed and these are deposited in a scattered pattern (Figure 1.2). Competition between individuals may stimulate the cheek pouch use as, without competition, cercopithecines would tend to stay where they feed, keeping food for shorter duration in their cheek pouches, and spitting-out seeds under the parent tree. First, for most species, troop size influences conspecific competition. Indeed primate food is mainly distributed in a patchy way, so that, in a small patch of food, a larger troop means a greater number of competitors (Murray 1975; Oates 1987) and thus a more extensive cheek pouch use (Lambert 2005). Fission of the social unit enables the usually gregarious Cercopithecinae species (*Papio hamadryas* and *Theropithecus gelada* (Aureli et al. 2008; Chapman & Chapman 2000), and sometimes *Macaca fuscata* (Fukuda 1989)) to feed on smaller food patches without increasing the competition risk (Chapman & Chapman 2000). Consequently, in these species, the cheek pouch use seems to be more important in larger food patches where competition is higher due to a lower fission process probability. Second, the cheek pouches use can be variable between troops, depending on habitats (more or less scattered resources), but also between troop members. In his study, Fust (2008) showed that, in *Papio ursinus orientalis*, dominant animals used their pouches more often than subordinates. This pattern could be explained by increased competition due to the more central position occupied by the dominant male within the troop.

Finally, cercopithecines frequently occur in large groups (mostly around 20-40 individuals but 80 individuals in *Papio cynocephalus*, 112 in *Miopithecus talapoin*, and 320 in *Theropithecus gelada* (Chapman & Chapman 2000)). Consequently, these groups may disperse large numbers of seeds. Moreover, studies on *Macaca silenus* (Menon & Poirier 1996; Singh et al. 2002) and *Macaca radiata* (Singh & Vinathe 1990) showed that groups living in a disturbed habitat were larger than groups in protected habitats. Thus, groups of some cercopithecine species could disperse more seeds in degraded habitats. Therefore, even if the way they disperse seeds turned out to be rather inefficient, they could play a critical role in forest restoration.

Conclusion

The high rate of deforestation threatens many frugivorous species' survival and, among them, primates are particularly vulnerable (Chapman et al. 2006; Nahallage et al. 2008). Nevertheless, some species are more resilient than others to human disturbances. This is the case of cercopithecines, which are often the only large seed dispersers remaining in some fragmented forests (Corlett 2002; Onderdonk 2000). However, most cercopithecine populations are decreasing, in part from deforestation, loss of resources and isolation, and in part from the increasing hunting and human-wildlife conflicts. Thirteen cercopithecine species are already considered endangered or critically endangered in the IUCN red list (2011) (Appendix 1.1). Given their potential role as seed dispersers (Dominy & Duncan 2005; Kaplin & Lambert 2002), their loss could have disastrous effects on tropical forest maintenance and regeneration (Chapman & Onderdonk 1998; Laurance 2005). Studies bringing more information on their dispersal role and how it may change in disturbed habitats are urgently needed, all the more reason that conservationists face a dilemma: cercopithecines may be invaluable seed dispersers but are engaged in too many conflicts with human populations. A better understanding of human-cercopithecines' conflicts could lead to management plans which could stop the continuous decrease of Cercopithecinae populations recorded over the last twenty years throughout much of their range (IUCN 2011). Their conservation could be the first step to the regeneration of degraded Asian and African forests.

Acknowledgments

We thank Lee Olsen for his valuable comments on previous drafts of this manuscript.

Appendix

Appendix 1.1. Main eco-ethological characteristics of Cercopithecinae species. Diet: Fr: frugivorous, Om: omnivorous, Fl; folivorous, Gr: granivorous; Cheek pouches: CP; Tolerance: T+: highly tolerant species are able to survive in highly disturbed habitats (*e.g.* urban areas); T-: tolerant species are able to survive in disturbed habitats (*e.g.* rural areas, plantations, young secondary forests, fragments); I: species know to be intolerant; underlined: endangered or critically endangered species; *: data deficient; -: no data; ( ): data supposed given information found in the literature.

Species	Area	Habitat	Locomotion	Diet	Home range (ha)	Daily range (m/d)	CP size	CP use	Tolerance
Allenopithecus nigroviridis	Sub-Saharan Africa[a]	Forest Wetlands[a]	Semi-terrestrial[h]	Fr-Om[b]	-	-	-	-	(I)[z]
Cercocebus agilis	Sub-Saharan Africa[a]	Forest[a]	Semi-terrestrial[c]	Fr-Om[c]	303[c]	1155[c]	Large[d]	High[d]	-
C. atys	Sub-Saharan Africa[a]	Forest Savanna[a]	Terrestrial[a]	Fr-Om[b]	500[b]	2200[b]	Large[d]	High[d]	T-[a]
*C. chrysogaster**	Sub-Saharan Africa[a]	Forest[a]	(Semi-terrestrial)	(Fr-Om)[b]	-	-	Large[d]	High[d]	-
C. galeritus	Sub-Saharan Africa[a]	Forest[a]	Semi-terrestrial[a]	Fr-Om[e]	17-47[e]	1040-1395[e]	Large[d]	High[d]	T-[e]
C. sanjei	Sub-Saharan Africa[a]	Forest[a]	Semi-terrestrial[a]	Fr-Om[a]	240[b]	-	Large[d]	High[d]	T-[a]

C. torquatus	Sub-Saharan Africa[a]	Forest[a]	Semi-terrestrial[b]	Fr-Om[b]	200-247[b]	1000[b]	Large[d]	High[d]	T-[a]
Cercopithecus ascanius	Sub-Saharan Africa[a]	Forest[a]	Semi-terrestrial[b] Arboreal[h]	Fr-Om[b,f]	23-68[b]	1447-1916[b]	Large[d]	High[d]	T-[a]
C. campbelli	Sub-Saharan Africa[a]	Forest Savanna[a]	Semi-terrestrial[b, h]	Fr-Om[g]	3-67[b]	1155[b]	Large[d]	High[d,g]	T+[a]
C. cephus	Sub-Saharan Africa[a]	Forest[a]	Arboreal[a]	Fl-Om[a]	30-100[b]	1300[b]	Large[d]	High[d]	(T-)[a]
C. diana	Sub-Saharan Africa[a]	Forest[a]	Arboreal[a, h]	Fr-Om[g]	29-189[b]	1019-1892[b]	Large[d]	High[d,g]	(T-)[a]
C. dryas	Sub-Saharan Africa[a]	Forest[a]	Terrestrial[a]	(Fr-Om)[b]	-	-	Large[d]	High[d]	(I)[a]
C. erythrogaster	Sub-Saharan Africa[a]	Forest[a]	-	-	-	-	Large[d]	High[d]	-
C. erythrotis	Sub-Saharan Africa[a]	Forest[a]	(Semi-terrestrial)[b]	(Fr-Om)[b]	-	-	Large[d]	High[d]	-
C. hamlyni	Sub-Saharan Africa[a]	Forest[a]	Semi-terrestrial[h]	(Fr-Om)[b]	-	-	Large[d]	High[d]	(I)[aa]
C. lhoesti	Sub-Saharan Africa[a]	Forest[a]	Terrestrial[a, h]	Fl-Om[i]	117[i]	2092[i]	Large[d]	High[d]	T-[b]

C. mitis	Sub-Saharan Africa[a]	Forest[a]	Arboreal[h]	Fr-Om[i]	88[i]	1307[i]	Large[d]	High[d]	T-[j]
C. mona	Sub-Saharan Africa[a]	Forest[a]	Arboreal[h]	Fr-Om[b]	25-100[b]	-	Large[d]	High[d]	T-[a]
C. neglectus	Sub-Saharan Africa[a]	Forest[a]	Semi-terrestrial[h]	Fr-Om[b]	4-10[b]	250-1010[b]	Large[d]	High[d]	I[bb]
C. nictitans	Sub-Saharan Africa[a]	Forest[a]	Arboreal[h]	Fr-Om[k]	140[b]	1825[b]	Large[d]	High[d]	(I)[cc]
C. petaurista	Sub-Saharan Africa[a]	Forest Shrubland[a]	Arboreal[h]	Fr-Om[g]	41-94[b]	1051[b]	Large[d]	High[d]	T-[a]
C. pogonias	Sub-Saharan Africa[a]	Forest[a]	Arboreal[h]	Fr-Om[b]	55-100[b]	1600[b]	Large[d]	High[d]	(I)[cc]
C. preussi	Sub-Saharan Africa[a]	Forest Grassland[a]	Terrestrial[h]	Fr-Om[b]	-	-	Large[d]	High[d]	-
C. sclateri	Sub-Saharan Africa[a]	Forest Shrubland[a]	Arboreal[b]	Fr-Om[a]	-	-	Large[d]	High[d]	T-[a]
C. solatus	Sub-Saharan Africa[a]	Forest[a]	Terrestrial[h]	Fr-Om[a]	-	-	Large[d]	High[d]	(T-)[a]
Chlorocebus aethiops	Sub-Saharan Africa[a]	Savanna Grasslands[a]	Semi-terrestrial[h]	Om[b]	23-90[b]	200-2540[b]	Medium[d]	High[d]	T+[a]

C. cynosuros	Sub-Saharan Africa^{a}	Forest Savanna^{a}	Semi-terrestrial^{b}	-	-	-	Medium^{d}	High^{d}	T+^{a}
C. djamdjamensis	Sub-Saharan Africa^{a}	Forest^{a}	Semi-terrestrial^{a}	Fl-Om^{b}	8-18^{b}	724-1288^{b}	Medium^{d}	High^{d}	(I)^{a}
C. pygerythrus	Sub-Saharan Africa^{a}	Forest Savanna Shrubland^{a}	Semi-terrestrial^{b}	Om^{b}	23-60^{b}	200-1632^{b}	Medium^{d}	High^{d}	T+^{a}
C. sabaeus	Sub-Saharan Africa^{a}	Forest Savanna^{a}	Semi-terrestrial^{b}	Fr-Om^{b}	15-164^{b}	2000-11,000^{b}	Medium^{d}	High^{d}	T+^{a}
C. tantalus	Sub-Saharan Africa^{a}	Forest Savanna^{a}	Semi-terrestrial^{b}	Om^{b}	43-90^{b}	1300-2540^{b}	Medium^{d}	High^{d}	T+^{a}
Erythrocebus patas	Sub-Saharan Africa^{a}	Savanna Shrubland Grassland^{a}	Terrestrial^{h}	Om^{a}	2340-4000^{b}	3188-4220^{b}	Medium^{d}	Low^{d}	T-^{a}
Lophocebus albigena	Sub-Saharan Africa^{a}	Forest^{a}	Arboreal^{a}	Fr-Om^{k}	200-410^{n}	900-1465^{m}	Large^{d}	Moderate^{f}	(I)
L. aterrimus	Sub-Saharan Africa^{a}	Forest^{a}	Arboreal^{a}	Fr-Om^{a}	48-70^{b}	-	Large^{d}	High^{d}	(I)
Macaca arctoides	SE Asia^{a}	Forest^{a}	Semi-terrestrial^{a}	Fr-Om^{a}	-	-	Large^{d}	High^{d}	(I)^{a}

M. assamensis	SE Asia[a]	Forest[a]	Semi-terrestrial[b]	Om[a]	95-470[b]	1900[b]	Large[d]	High[d]	(I)[a]
M. cyclopis	SE Asia[a]	Forest[a]	Semi-terrestrial[a]	Fr-Om[a,b]	130[b]	2065[b]	Large[d]	High[d]	T-[a]
M. fascicularis	SE Asia[a]	Forest Wetlands[a]	Semi-terrestrial[a]	Om[a]	7-300[b]	1900[o]	Large[d]	High[d]	T+[a]
M. fuscata	SE Asia[a]	Forest[a]	Semi-terrestrial[b]	Om[b]	214-797[b]	1218[b]	Large[d]	High[d]	T+[dd]
M. hecki	SE Asia[a]	Forest[a]	Semi-terrestrial[a]	(Fr-Om)[a]	-	-	Large[d]	High[d]	-
M. leonina	SE Asia[a]	Forest[a]	Semi-terrestrial[a]	Fr-Om[a]	83-347[b]	690-2240[b]	Large[d]	High[d]	T-[a]
M. maura	SE Asia[a]	Forest Grassland[a]	(Semi-terrestrial)	Fr-Om[a]	20[b]	-	Large[d]	High[d]	-
M. mulatta	SE Asia[a]	Forest Savanna Shrubland[a]	Semi-terrestrial[a]	Om[a]	130-1340[p]	1050-3050[p]	Large[d]	High[d]	T+[a]
M. munzala	SE Asia[a]	Forest[a]	Semi-terrestrial[a]	Fr-Om[a,b]	22[b]	1500[b]	Large[d]	High[d]	T-[a]
M. nemestrina	SE Asia[a]	Forest[a]	Semi-terrestrial[a]	Fr-Om[a]	62-828[q]	902-2960[q]	Large[d]	High[d]	T-[a]

M. nigra	SE Asia[a]	Forest[a]	Semi-terrestrial[b]	Fr-Om[a]	175-314[b]	1750-3140[b]	Large[d]	High[d]	I[r]
M. nigrescens	SE Asia[a]	Forest[a]	(Semi-terrestrial)	Fr-Om[a]	-	515-1240[b]	Large[d]	High[d]	T-[a]
M. ochreata	SE Asia[a]	Forest[a]	Semi-terrestrial[b]	Fr-Om[a]	29-85[b]	-	Large[d]	High[d]	T-[ee]
M. pagensis	SE Asia[a]	Forest[a]	Semi-terrestrial[b]	Fr-Om[a]	-	-	Large[d]	High[d]	(T-)[a]
M. radiata	SE Asia[a]	Forest Savanna Shrubland[a]	Semi-terrestrial [a]	Fr-Om[a]	2-500[b]	710-1300[b]	Large[d]	High[d]	T+[a]
M. siberu	SE Asia[a]	Forest[a]	Semi-terrestrial[b]	Fr-Om[b]	530[b]	-	Large[d]	High[d]	(T-)[a]
M. silenus	SE Asia[a]	Forest[a]	Arboreal[a]	Fr-Om[a]	131[s]	750-2500[s]	Large[d]	High[d]	T-[s,t]
M. sinica	SE Asia[a]	Forest[a]	Arboreal[a]	Fr-Om[a]	41[b]	500-2000[b]	Large[d]	High[d]	T- [ff]
M. sylvanus	North-Africa[a]	Forest Shrubland Rocky areas[a]	Semi-terrestrial[b]	Gr-Om[a]	200-720[b]	2000-9000[b]	Large[d]	High[d]	(I)[a]
M. thibetana	SE Asia[a]	Forest Caves[a]	Semi-terrestrial[a]	Fr-Om[a]	500[b]	-	Large[d]	High[d]	(I)[b]

M. tonkeana	SE Asia[a]	Forest[a]	Semi-terrestrial[a]	Fr-Om[a]	67-143[u]	-	Large[d]	High[d]	T-[u]
Mandrillus leucophaeus	Sub-Saharan Africa[a]	Forest Savanna[a]	Semi-terrestrial[a]	Fr-Om[v]	-	-	-	-	(I)[a]
M. sphinx	Sub-Saharan Africa[a]	Forest[a]	Semi-terrestrial[a]	Fr-Om[l]	500-2850[b]	2003-3263[b]	-	-	(T-)[a]
Miopithecus ogouensis	Sub-Saharan Africa[a]	Forest[a]	Semi-terrestrial[a]	Fr-Om[a]	110-140[b]	1500-2950[b]	Medium[d]	High[d]	T-[a]
M. talapoin	Sub-Saharan Africa[a]	Forest Wetlands[a]	Semi-terrestrial[a]	Fr-Om[a]	-	-	Medium[d]	High[d]	-
Papio anubis	Sub-Saharan Africa[a]	Forest Savanna Shrubland Grassland[a]	Terrestrial[b]	Om[a]	900-4357[b]	1200-5637[b]	Small[d]	Low[d]	T-[a]
P. cynocephalus	Sub-Saharan Africa[a]	Forest Savanna Shrubland[a]	Terrestrial[b]	Om[a]	2408[b]	3400-7200[b]	Small[d]	Low[d]	T-[a]
P. hamadryas	Sub-Saharan Africa[a]	Shrubland Grassland Rocky areas[a]	Terrestrial[w]	Om[a]	3000[w]	7500[w]	Small[d]	Low[d]	-

P. papio	Sub-Saharan Africa[a]	Forest Savanna Grassland[a]	Terrestrial[b]	Fr-Om[b]	2000-4500[b]	4000-13,000[b]	Small[d]	Low[d]	-
P. ursinus	Sub-Saharan Africa[a]	Forest Savanna Shrubland Grassland Desert[a]	Terrestrial[a]	Om[a]	500-1917[b]	4670-10,460[x]	Small[d]	Moderate[y]	-
Rungwecebus kipunji	Sub-Saharan Africa[a]	Forest[a]	Arboreal[b]	Om[a]	306[b]	1293[b]	-	-	(I)
Theropithecus gelada	Sub-Saharan Africa[a]	Grassland Rocky areas[a]	Terrestrial[a]	Fl[a]	84-928[b]	2500[x]	Small[d]	Low[d]	I[a]

[a](IUCN 2011); [b](Rowe & Myers 2011); [c](Shah 2003); [d](Murray 1975); [e](Wieczkowski 2005); [f](Lambert 2005); [g](Buzzard 2006); [h](Sargis et al. 2008); [i](Kaplin 2001); [j](Lawes 2002); [k](Poulsen et al. 2002); [l](Tutin et al. 1997a); [m](Olupot et al. 1994); [n](Onderdonk 2000); [o](Wheatley 1980); [p](Makwana 1978); [q](Caldecott 1986); [r](Rosenbaum et al. 1998); [s](Kurup & Kumar 1993); [t](Umapathy & Kumar 2000); [u](Riley 2007); [v](Astaras & Waltert 2010); [w](Swedell 2002); [x](Wrangham et al. 1993); [y](Fust 2008); [z](Maisels et al. 2006); [aa](Thomas 1991); [bb](Brennan 1985); [cc](Blom et al. 2005); [dd](Fukuda 2004); [ee](Riley et al. 2007); [ff] (Dittus 1975)

Literature cited

Andresen, E. & Levey, D. J. 2004. Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia*, 139, 45-54.

Astaras, C. & Waltert, M. 2010. What does seed handling by the drill tell us about the ecological services of terrestrial cercopithecines in African forests? *Animal Conservation*, 13, 568-578.

Aureli, F., Shaffner, C., Boesch, C., Bearder, S., Call, J., Chapman, C., Connor, R., Di Fiore, A., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P. C., Lehmann, J., Manson, J. H., Ramos-Fernández, G., Strier, K. B. & van Schaik, C. P. 2008. Fission-fusion dynamics: new research frameworks. *Current Anthropology*, 49, 627-654.

Blom, A., Zalinge, R. v., Heitkönig, I. M. A. & Prins, H. H. T. 2005. Factors influencing the distribution of large mammals within a protected central African forest. *Oryx*, 39, 381-388.

Boulton, A. M., Horrocks, J. A. & Baulu, J. 1996. The Barbados vervet monkey (*Cercopithecus aethiops sabaeus*): changes in population size and crop damage, 1980-1994. *International Journal of Primatology*, 17, 831-844.

Brennan, E. J. 1985. De Brazza's monkeys (*Cercopithecus neglectus*) in Kenya: Census, distribution, and conservation. *American Journal of Primatology*, 8, 269-277.

Brodie, J. F., Helmy, O. E., Brockelman, W. Y. & Maron, J. L. 2009. Functional differences within a guild of tropical mammalian frugivores. *Ecology*, 90, 688-698.

Brook, B. W., Sodhi, N. S. & Ng, P. K. L. 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature*, 424, 420-423.

Brotcorne, F., Wandia, I. N., Rompis, A. L. T., Soma, I. G., Suartha, I. N. & Huynen, M. C. 2011. Recent demographic and behavioural data of *Macaca fascicularis* at Padangtegal, Bali (Indonesia). In: *Monkeys on the edge: ecology and management of long-tailed macaques and their interface with humans* (Ed. by Gumert, M. D., Fuentes, A. & Jones-Engel, L.), pp. 180-183. Cambridge Cambridge University Press.

Butler, R. A. & Laurance, W. F. 2008. New strategies for conserving tropical forests. *Trends in Ecology and Evolution*, 23, 469-472.

Buzzard, P. J. 2006. Cheek pouch use in relation to interspecific competition and predator risk for three guenon monkeys (*Cercopithecus* spp.). *Primates*, 47, 336-341.

Caldecott, J. O. 1986. *An ecological and behavioural study of the pig-tailed macaque*. Basel: Karger.

Chapman, C. A. 1995. Primate seed dispersal: Coevolution and conservation implications. *Evolutionary Anthropology*, 4, 74-82.

Chapman, C. A. & Chapman, L. J. 1995. Survival without dispersers: seeding recruitment under parents. *Conservation Biology*, 9, 675-678.

Chapman, C. A. & Chapman, L. J. 2000. Determinants of group size in primates: the importance of travel costs. In: *On the move: How and why animals travel in groups* (Ed. by Boinski, S. & Garber, P. A.), pp. 24-42. Chicago University of Chicago Press.

Chapman, C. A., Lawes, M. J. & Eeley, H. A. C. 2006. What hope for African primate diversity? *African Journal of Ecology*, 44, 116-133.

Chapman, C. A. & Onderdonk, D. A. 1998. Forests without primates: Primate/plant codependency. *American Journal of Primatology*, 45, 127-141.

Chapman, C. A. & Russo, S. E. 2007. Primate seed dispersal: Linking behavioral ecology with forest community structure. In: *Primates in perspective* (Ed. by Campbell, C. J., Fuentes, A. F., MacKinnon, K. C., Panger, M. & Bearder, S.), pp. 510-525. Oxford: Oxford University Press.

Chapman, H. M., Goldson, S. L. & Beck, J. 2009. Postdispersal removal and germination of seed dispersed by *Cercopithecus nictitans* in a West African montane forest. *Folia primatologica*, 81, 41-50.

Chauhan, A. & Pirta, R. S. 2010. Agonistic interactions between humans and two species of monkeys (rhesus monkey *Macaca mulatta* and hanuman langur *Semnopithecus entellus*) in Shimla, Himachal Pradesh. *Journal of Psychology*, 1, 9-14.

Cipollini, M. L. & Levey, D. J. 1997. Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *The American Naturalist*, 150, 346-372.

Corlett, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews*, 73, 413-448.

Corlett, R. T. 2002. Frugivory and seed dispersal in degraded tropical East Asian landscape. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 451-465. New York: CABI Publishing.

Corlett, R. T. 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica*, 39, 292-303.

Corlett, R. T. & Lucas, P. W. 1990. Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*). *Oecologia*, 82, 166-171.

Cowlishaw, G. & Dunbar, R. 2000. *Primate conservation biology*. Chicago and London: The University of Chicago Press.

Cramer, J. M., Mesquita, R. C. G. & Williamson, G. B. 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biological Conservation*, 137, 415-423.

Culot, L., Huynen, M.-C. & Heymann, E. W. 2009. Short-term post-dispersal fate of seeds defecated by two small primate species (*Saguinus mystax* and *Saguinus fuscicollis*) in the Amazonian forest of Peru. *Journal of Tropical Ecology*, 25, 229-238.

da Silva, J. M. C., Uhl, C. & Murray, G. 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conservation Biology*, 10, 491-503.

Dirzo, R. 2001. Plant-animal interactions: Lessons for our understanding of nature, and implications for biodiversity conservation. In: *Ecology: Achievement and challenge* (Ed. by Press, M. C., J.Huntley, N. & Levin, S.), pp. 319-355. Oxford, UK: Blackwell Science.

Dittus, W. P. J. 1975. Populationd dynamics of the toque monkey, *Macaca sinica*. In: *Socioecology and psychology of primates* (Ed. by Tuttle, R. H.), pp. 125-151. The Hague: Mouton Publishers.

Dominy, N. J. & Duncan, B. W. 2005. Seed-spitting primates and the conservation and dispersion of large-seeded trees. *International Journal of Primatology*, 26, 631-649.

Donatti, C. I., Guimarães, P. R., Galetti, M., Pizo, M. A., Marquitti, F. M. D. & Dirzo, R. 2011. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecology Letters*, 14, 773-781.

Duncan, R. S. & Chapman, C. A. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications*, 9, 998-1008.

Duncan, R. S. & Chapman, C. A. 2002. Limitations of animal seed dispersal for enhancing forest succession on degraded lands. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 437-450. New York: CAB International.

Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P. & Sodhi, N. S. 2009. The sixth mass coextinction: are most endangered species parasites and mutualists? *Proceedings of the Royal Society B*, 276, 3037-3045.

Fukuda, F. 1989. Habitual fission-fusion and social organization of the Hakone troop of Japanese macaques in Kanagawa prefecture, Japan *International Journal of Primatology*, 10, 419-439.

Fukuda, F. 2004. Dispersal and environmental disturbance in japanese macaques (*Macaca fuscata*). *Primate Report*, 68, 53-69.

Fust, P. 2008. Function and use of cheek pouches in cape chacma baboon (*Papio ursinus orientalis*) population in Cape Floral Kingdom, South Africa. Research Dissertation, Napier University.

Gross-Camp, N. & Kaplin, B. A. 2005. Chimpanzee (*Pan troglodytes*) seed dispersal in an Afromontane forest: microhabitat influences on the postdispersal fate of large seeds. *Biotropica*, 37, 641-649.

Gross-Camp, N. & Kaplin, B. A. 2011. Differential seed handling by two African primates affects seed fate and establishment of large-seeded trees. *Acta Oecologica*, 37, 578-586.

Hill, C. M. 2000. Conflict of interest between people and baboons: crop raiding in Uganda. *International Journal of Primatology*, 21, 299-315.

Hill, C. M. & Webber, A. D. 2010. Perceptions of nonhuman primates in human-wildlife conflict scenarios. *American Journal of Primatology*, 72, 919-924.

Howe, H. F. 1984. Constraints on the evolution of mutualisms. *The American Naturalist*, 123, 764-777.

IUCN. 2011. IUCN Red List of Threatened Species. Version 2011.1. http://www.iucnredlist.org Downloaded on 26/10/2011.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist*, 104, 501-528.

Johns, A. D. & Skorupa, J. P. 1987. Responses of rain-forest primates to habitat disturbance: a review. *International Journal of Primatology*, 8, 157-191.

Jordano, P., García, C., Godoy, J. A. & García-Castaño, J. L. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 3278-3282.

Kaplin, B. A. 2001. Ranging behavior of two species of guenons (*Cercopithecus lhoesti* and *C. mitis doggetti*) in the Nyungwe Forest Reserve, Rwanda. *International Journal of Primatology*, 22, 521-548.

Kaplin, B. A. & Lambert, J. E. 2002. Effectiveness of seed dispersal by *Cercopithecus* Monkeys: Implications for seed input into degraded areas. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 351-364. New York: CABI Publishing.

Kaplin, B. A. & Moermond, T. C. 1998. Variation in seed handling by two species of forest monkeys in Rwanda. *American Journal of Primatology*, 45, 83-101.

Kirika, J. M., Bleher, B., Böhning-Gaese, K., Chira, R. & Farwig, N. 2008. Fragmentation and local disturbance of forests reduce frugivore diversity and fruit removal in *Ficus thonningii* trees. *Basic and Applied Ecology*, 9, 663-672.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T. & Noma, N. 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133, 559-572.

Kunz, B. K. & Linsenmair, K. E. 2008. Diet and behavioural ecology of olive baboons in the Comoé National Park. *Folia Primatologica*, 79, 31-51.

Kurup, G. U. & Kumar, A. 1993. Time budget and activity patterns of the lion-tailed macaque (*Macaca silenus*). *International Journal of Primatology*, 14, 27-39.

Kwit, C., Levey, D. J. & Greenberg, C. H. 2004. Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. *Oikos*, 107, 303-308.

Lambert, J. E. 1998. Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evolutionary Anthropology*, 7, 8-20.

Lambert, J. E. 1999. Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *American Journal of Physical Anthropology*, 109, 365-386.

Lambert, J. E. 2001. Red-tailed guenons (*Cercopithecus ascanius*) and strychnos mitis: evidence for plant benefits beyond seed dispersal. *International Journal of Primatology*, 22, 189-201.

Lambert, J. E. 2002. Digestive retention times in forest guenons (*Cercopithecus* spp.) with reference to chimpanzees (*Pan troglodytes*). *International Journal of Primatology*, 23, 1169-1185.

Lambert, J. E. 2005. Competition, predation, and the evolutionary significance of the cercopithecine cheek pouch: the case of *Cercopithecus* and *Lophocebus*. *American Journal of Physical Anthropology*, 126, 183-192.

Lambert, J. E. & Chapman, C. A. 2005. The fate of primate-dispersed seeds: deposition pattern, dispersal distance and implications for conservation. In: *Seed Fate - Predation, Dispersal and Seedling Establishment* (Ed. by Forget, P.-M., Lambert, J. E., Hulme, P. E. & Vander Wall, S. B.), pp. 137-150. Cambridge: CAB International.

Laurance, W. F. 2005. The alteration of biotic interactions in fragmented tropical forests. In: *Biotic interactions in the tropics: their role in the maintenance of species diversity* (Ed. by Burslem, D. F. R. P., Pinard, M. A. & Hartley, S. E.). Cambridge Cambridge University Press.

Laurance, W. F., Croes, B. M., Tchignoumba, L., Lahm, S. A., Alonso, A., Lee, M. E., Campbell, P. & Ondzeano, C. 2006. Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology*, 20, 1251-1261.

Lawes, M. J. 2002. Conservation of fragmented populations of *Cercopithecus mitis* in South Africa: the role of reintroduction, corridors and metapopulation ecology In: *The guenons: diversity and adaptation in African monkeys* (Ed. by Glenn, M. E. & Cords, M.), pp. 375-392. New York: Kluwer Academic/Plenum Publishers.

Lee, P. C. & Priston, N. E. C. 2005. Human attitudes to primates: perceptions of pests, conflict and consequences for primate conservation. In: *Commensalism and conflict: the human primate interface* (Ed. by Paterson, J. D. & Wallis, J.), pp. 1-23. Winnepeg: Hignell Printing.

Levey, D. J. & Byrne, M. M. 1993. Complex ant-plant interactions: rain-forest ants as secondary dispersers and post-dispersal seed predators. *Ecology*, 74, 1802-1812.

Li, H. & Zhang, Z. 2007. Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae). *Forest Ecology and Management*, 242, 511-517.

Lucas, P. W. & Corlett, R. T. 1998. Seed dispersal by long-tailed macaques. *American Journal of Primatology*, 45, 29-44.

Maisels, F., Blake, S., Fay, M., Mobolambi, G. & Yako, V. 2006. A Note on the distribution of Allen’s swamp monkey, *Allenopithecus nigroviridis*, in northwestern Congo. *Primate Conservation*, 21, 93-95.

Makwana, S. C. 1978. Field ecology and behaviour of the rhesus macaque (*Macaca mulatta*): I. Group composition, home range, roosting sites, and foraging routes in the Asarori Forest. *Primates*, 19, 483-492.

McConkey, K. R. & Brockelman, W. Y. 2011. Non-redundancy in the dispersal network of a generalist tropical forest tree. *Ecology*, 92, 1492-1502.

McConkey, K. R. & Drake, D. R. 2006. Flying foxes cease to function as seed dispersers long before they become rare. *Ecology,* 87, 271-276.

Medellin, R. A. & Gaona, O. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica*, 31, 478-485.

Menon, S. & Poirier, F. E. 1996. Lion-tailed macaques (*Macaca silenus*) in a disturbed forest fragment: activity patterns and time budget. *International Journal of Primatology*, 17, 969-985.

Muller-Landau, H. C. 2007. Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. *Biotropica*, 39, 372-284.

Murray, P. 1975. The role of cheek pouches in cercopithecine monkey adaptative strategy. In: *Primate functional morphology and evolution* (Ed. by Tuttle, R. H.), pp. 151-194. The Hague: Mouton.

Muscarella, R. & Fleming, T. H. 2007. The role of frugivorous bats in tropical forest succession. *Biological Reviews*, 82, 573-590.

Nahallage, C. A. D., Huffman, M. A., Kuruppu, N. & Weerasingha, T. 2008. Diurnal primates in Sri Lanka and people's perception of them. *Primate Conservation*, 23, 81-87.

Nakashima, Y., Lagan, P. & Kitayama, K. 2008. A study of fruit–frugivore interactions in two species of Durian (*Durio*, Bombacaceae) in Sabah, Malaysia. *Biotropica*, 40, 255-258.

Nathan, R. & Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, 15, 278-285.

Naughton-Treves, L. 1998. Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conservation Biology,* 12, 156-168.

Oates, J. F. 1987. Food distribution and foraging behavior. In: *Primate Societies* (Ed. by Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T.), pp. 197-209. Chicago University of Chicago Press.

Olupot, W., Chapman, C. A., Brown, C. H. & Waser, P. M. 1994. Mangabey (*Cercocebus albigena*) population density, group size, and ranging: a twenty-year comparison. *American Journal of Primatology*, 32, 197-205.

Onderdonk, D. A. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *International Journal of Primatology*, 21, 587-611.

Otani, T. 2004. Effects of macaque ingestion on seed destruction and germination of a fleshy-fruited tree, *Eurya emarginata*. *Ecological Research*, 19, 495-501.

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L., Chini, L., Cooper, H. D., Gilman, E. L., Guénette, S., Hurtt, G. C., Huntington, H. P., Mace, G. M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R. J., Sumaila, U. R. & Walpole, M. 2010. Scenarios for global biodiversity in the 21st century. *Science*, 330, 1496-1501.

Poulsen, J. R., Clark, C. J., Connor, E. F. & Smith, T. B. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology*, 83, 228-240.

Pringle, E. G., Álvarez-Loayza, P. & Terborgh, J. 2007. Seed characteristics and susceptibility to pathogen attack in tree seeds of the Peruvian Amazon. *Plant Ecology*, 193, 211-222.

Priston, N. E. C. 2005. Crop-raiding by *Macaca Ochreata Brunnescens* in Sulawesi: reality, perceptions and outcomes for conservation, University of Cambridge

Ram, S., Venkatachalam, S. & Sinha, A. 2003. Changing social strategies of wild female bonnet macaques during natural foraging and on provisioning. *Current Science*, 84, 780-790.

Redford, K. H. & Feinsinger, P. 2001. The half-empty forest: sustainable use and the ecology of interactions. In: *Conservation of Exploited Species* (Ed. by Reynolds, J. D., Mace, G. M., Redford, K. H., Robinson, J. G., Gosling, M. L., Cowlishaw, G., Woodroffe, R. & Gittleman, J.), pp. 370-400. Cambridge: Cambridge University Press.

Richard, A. F., Goldstein, S. J. & Dewar, R. E. 1989. Weed macaques: the evolutionary implications of macaque feeding ecology. *International Journal of Primatology*, 10, 569-594.

Riley, E. P. 2007. Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. *International Journal of Primatology*, 28, 107-133.

Riley, E. P., Suryobroto, B. & Maestripieri, D. 2007. Distribution of *Macaca ochreata* and identification of mixed ochreata-tonkeana groups in South Sulawesi, Indonesia. *Primate Conservation*, 22, 129-133.

Rodman, P. S. 1979. Skeletal differentiation of *Macaca fascicularis* and *Macaca nemestrina* in relation to arboreal and terrestrial quadrupedalism. *American Journal of Physical Anthropology*, 51, 51-62.

Rosenbaum, B., O'Brien, T. G., Kinnaird, M. & Supriatna, J. 1998. Population densities of Sulawesi crested black macaques (*Macaca nigra*) on Bacan and Sulawesi, Indonesia: effects of habitat disturbance and hunting. *American Journal of Primatology*, 44, 89-106.

Rowe, N. & Myers, M. 2011. All the World's Primates. www.alltheworldsprimates.org. Primate Conservation Inc. Charlestown RI. Downloaded on 10/10/2011. Charlestown RI.

Saj, T. L., Sicotte, P. & Paterson, J. D. 2001. The conflict between vervet monkeys and farmers at the forest edge in Entebbe, Uganda. *African Journal of Ecology*, 39, 195-199.

Sargis, E. J., Terranova, C. J. & Gebo, D. L. 2008. Evolutionary morphology of the guenon postcranium and its taxonomic implications. In: *Mammalian evolutionary morphology: A tribute to Frederick S. Szalay* (Ed. by Sargis, E. J.), pp. 361-372. New York: Springer-Verlag New York Inc.

Savini, T. & Kanwatanakid-Savini, C. 2011. Feeding overlap and seed dispersal efficiency between sympatric hornbills and gibbons in Thailand. *The Raffles Bulletin of Zoology*, 24, 115-122.

Schupp, E. W., Jordano, P. & Gómez, J. M. 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist*, 188, 333-353.

Setchell, J. M. & Curtis, D. J. 2003. *Field and laboratory methods in primatology: practical guide*. Cambridge: Cambridge University Press.

Shah, N. F. 2003. Foraging strategies in two sympatric mangabey species (*Cercocebus agilis* and *Lophocebus albigena*). PhD, Stony Brook University.

Sillero-Zubiri, C. & Switzer, D. 2001. *Crop raiding primates: Searching for alternative, humane ways to resolve conflict with farmers in Africa*: People and Wildlife Initiative. Wildlife Conservation Research Unit, Oxford University.

Singh, M., Singh, M., Kumar, M. A., Kumara, H. N., Sharma, A. K. & Kaumanns, W. 2002. Distribution, population structure, and conservation of lion-tailed macaques (*Macaca* *silenus*) in the Anaimalai Hills, Western Ghats, India. *American Journal of Primatology*, 57, 91-102.

Singh, M. & Vinathe, S. 1990. Inter-population differences in the time budgets of bonnet monkeys (*Macaca radiata*). *Primates*, 31, 589-596.

Strum, S. C. 2010. The development of primate raiding: implications for management and conservation. *International Journal of Primatology*, 31, 133-156.

Swedell, L. 2002. Ranging behavior, group size and behavioral flexibility in Ethiopian hamadryas baboons (*Papio hamadryas hamadryas*). *Folia primatologica*, 73, 95-103.

Thomas, S. C. 1991. Population densities and patterns of habitat use among anthropoid primates of the Ituri Forest, Zaire. *Biotropica*, 23, 68-83.

Traveset, A. 1998. Effect of seed passage through vertebrate frugivores’ guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics*, 1/2, 151-190.

Traveset, A. & Verdú, M. 2002. A meta-analysis of the effect of gut treatment on seed germination. In: *Seed dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 339-350. New York: CAB International.

Tsujino, R. & Yumoto, T. 2009. Topography-specific seed dispersal by Japanese macaques in a lowland forest on Yakushima Island, Japan. *Journal of Animal Ecology*, 78, 119-125.

Tutin, C. E. G., Ham, R. M., White, L. J. T. & Harrison, M. J. S. 1997a. The primate community of the Lopé reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology*, 42, 1-24.

Tutin, C. E. G., White, L. J. T. & Mackanga-Missandzou, A. 1997b. The use by rain forest mammals of natural forest fragments in an Equatorial African savanna. *Conservation Biology*, 11, 1190-1203.

Twinomugisha, D., Chapman, C. A., Lawes, M. J., O'Driscoll Worman, C. & Danish, L. M. 2006. How does the golden monkey of the Virungas cope in a fruit scarce environment? In: *Primates of Western Uganda* (Ed. by Newton-Fisher, N. E., Notman, H., Reynolds, V. & Paterson, J. D.), pp. 45-60. New York: Springer.

Umapathy, G. & Kumar, A. 2000. Impacts of the habitat fragmentation on time budget and feeding ecology of lion-tailed macaque (*Macaca silenus*) in rain forest fragments of Anamalai Hills, South India. *Primate Report*, 58, 67-82.

Vanthomme, H., Bellé, B. & Forget, P. M. 2010. Bushmeat hunting alters recruitment of large-seeded plant species in Central Africa. *Biotropica*, 42, 672-679.

Vulinec, K., Lambert, J. E. & Mellow, D. J. 2006. Primate and dung beetle communities in secondary growth rain forests: implications for conservation of seed dispersal systems. *International Journal of Primatology*, 27, 855-879.

Warren, Y. 2008. Crop-raiding baboons (*Papio anubis*) and defensive farmers: a West African perspective. *West African Journal of Applied Ecology*, 14, 1-11.

Weyher, A. H., Ross, C. & Semple, S. 2006. Gastrointestinal parasites in crop raiding and wild foraging *Papio anubis* in Nigeria. *International Journal of Primatology*, 27, 1519-1534.

Wheatley, B. P. 1980. Feeding and ranging of East Bornean *Macaca fascicularis*. In: *The macaques: studies in ecology, behavior and evolution* (Ed. by Lindburg, D. G.), pp. 215-246. New York: Van Nostrand Reinhold Company.

Wieczkowski, J. 2005. Comprehensive conservation profile of Tana mangabeys. *International Journal of Primatology*, 26, 651-660.

Willson, M. & Traveset, A. 2000. The ecology of seed dispersal. In: *Seeds: the ecology of regeneration in plant communities* (Ed. by Fenner, M.), pp. 85-110. Wallingford, UK: CAB International.

Wilson, D. E. & Reeder, D. M. 2005. *Mammal species of the world. A taxonomic and geographic reference*, 3rd edition edn: Johns Hopkins University Press.

Woodroffe, R., Thirgood, S. & Rabinowitz, A. 2005. The impact of human-wildlife conflict on natural systems. In: *People and wildlife: conflict or coexistence?* (Ed. by Woodroffe, R., Thirgood, S. & Rabinowitz, A.). Cambridge: Cambridge University Press.

Wrangham, R. W., Conklin-Brittain, N. L. & Hunt, K. D. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology*, 19, 949-970.

Wrangham, R. W., Gittleman, J. L. & Chapman, C. A. 1993. Constraints on group size in primates and carnivores: population density and day-range as assays of expoitation competition. *Behavioral Ecology and Sociobiology*, 32, 199-209.

Wright, S. J., Hernandéz, A. & Condit, R. 2007. The bushmeat harvest alters seedling banks by favoring lianas, large seeds, and seeds dispersed by bats, birds, and wind. *Biotropica*, 39, 363-371.

Wright, S. J. & Muller-Landau, H. C. 2006. The future of tropical forest species. *Biotropica*, 38, 287-301.

Wright, S. J., Zeballos, H., Domínguez, I., Gallardo, M. M., Moreno, M. C. & Ibáñez, R. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology*, 14, 227-239.

Yumoto, T., Noma, N. & Maruhashi, T. 1998. Cheek-pouch dispersal of seeds by Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, 39, 325-338.

In the previous chapter, we showed that most cercopithecine species are thought to provide effective seed dispersal services due to their eco-ethological and physical characteristics.

~~~

In the next chapter, we will focus on a little known cercopithecine species, *Macaca leonina*, and study its seed dispersal effectiveness, from a quantitative and qualitative point of view.
~~~

CHAPTER 2

Frugivory and Seed Dispersal by Northern Pigtailed Macaques, *Macaca leonina*, in Thailand

Albert, A., Hambuckers, A., Culot, L., Savini, T., Huynen, M.-C. Frugivory and seed dispersal by northern pigtailed macaques, *Macaca leonina*, in Thailand. Submitted to Biotropica.

Résumé

La conservation des forêts tropicales requière une meilleure compréhension et quantification des interactions plantes-animaux. Il est particulièrement nécessaire d’étudier le rôle des frugivores dans le processus de dispersion des graines, étant donné les bénéfices que cette dispersion apporte à la plante en diminuant les risques de compétition et d’attaques par des pathogènes dépendants de la densité. En suivant une troupe de macaques à queue de cochon du Nord (*Macaca leonina*) habitués à l’homme dans le parc national de Khao Yai, Thaïlande, nous avons apporté des données sur ces disperseurs de graines, potentiellement nécessaires à au maintien et à la régénération des forêts, mais malheureusement considérés comme vulnérables. Les résultats montrent que les macaques à queue de cochon du Nord pouvaient disperser jusqu’à plusieurs milliers de graines, allant jusqu’à 58 mm de long, et venant des 126 espèces de fruits qu’ils consommaient. De plus, ils pouvaient disperser ces graines de forêt primaire en forêt secondaire, grâce à plusieurs techniques de manipulation telles que l’ingestion, le recrachage et le dépôt. Finalement, le passage des graines dans le tractus digestif avait un effet neutre ou positif sur la germination et la viabilité de ces mêmes graines pour 14 espèces sur les 21 testées. Les macaques observés dans cette étude satisfont donc à la plupart des exigences permettant de définir un disperseur efficace, en termes de quantité et de qualité de dispersion, et nous pouvons conclure à l’importance potentielle de *Macaca leonina* dans la régénération des forêts tropicales.

***Mots-clés* :** germination ; parc national de Khao Yai ; recrachage ; ingestion ; forêt tropicale humide.

Abstract

The conservation of tropical rainforests requires a better understanding and quantification of plant-animal interactions. In particular, the role of frugivorous species in the seed dispersal process has to be studied because plants benefit from seed dispersal as a way for the seeds to escape competition and density-dependent seed predators and pathogens. While following a troop of northern pigtailed macaques (*Macaca leonina*) habituated to humans in Khao Yai National Park, Thailand, we brought data about these seed dispersers which are potentially necessary for forest maintenance and regeneration but whose conservation status is unfortunately vulnerable. Results show that northern pigtailed macaques could disperse thousands of seeds, up to 58 mm in length, and coming from the 126 fruit species they eat. Especially, they could disperse them from primary to secondary forests, thanks to handling techniques such as swallowing, spitting, and dropping. Finally, the seed passage through their digestive tract had a neutral or positive effect on seed germination and viability for 14 species out of 21 tested. Macaques observed in this study satisfied, therefore, most requirements defining effective seed dispersers in both quantitative and qualitative terms. We can thus make conclusions pertaining to the potential importance of *Macaca leonina* in tropical rainforest regeneration.

Key words**:** germination; Khao Yai National Park; seed spitting; swallowing; tropical rainforest.

Introduction

Southeast Asia includes the 3rd most important biodiversity hotspot worldwide: the Indo-Burma region. This area features exceptional concentrations of endemic species, but is experiencing exceptional loss of habitat, mainly resulting from high deforestation rate (Laurance 2007; Myers et al. 2000; Sodhi et al. 2004). One consequence is the loss of many animal species, mainly large frugivores, essential dispersal agents for large-seeded plant species (Cordeiro & Howe 2001).

Today, many Southeast Asian countries are aware of their forests degraded condition, and want to save the remaining primary forest and regenerate the degraded areas through natural or artificial reforestation (Laurance 2007). Tropical rainforest conservation and restoration depend on an increased knowledge of plant-animal interaction processes – particularly seed dispersal – and on measures to protect them (Corlett & Hau 2000; Forest Restoration Research Unit 2008; Parrotta 2000).

Many studies have already highlighted the primates’ role as seed dispersers (Chapman & Onderdonk 1998; Chaves et al. 2011; Garber & Lambert 1998), but their effectiveness in this service can be extremely variable between species and depends on environmental conditions. Most primates may disperse seeds by swallowing and dropping. Authors have shown some positive effects of swallowing on seed germination: (1) the fruit pulp removal, increasing seed germination (Otani 2004; Tang et al. 2008; Traveset & Verdú 2002) and often decreasing the risk of pathogen attacks (Lambert 2001; Pringle et al. 2007); (2) the mechanical and/or chemical seed coat scarification in the gut (Dew & Wright 1998; Traveset et al. 2001); and (3) the effect of fecal material surrounding the seeds, promoting germination and/or future seedling growth (Traveset & Verdú 2002). In addition, some primates generate a specific seed dispersal pattern. For instance, the Cercopithecinae cheek pouches enable them to store fruits and keep moving. After storage, fruits are returned one by one to the oral cavity for processing, ending with the seed being spat out (Corlett & Lucas 1990). This single deposit decreases the risk of attack by density-dependent predators and, thus, increases the germination probability. The cercopithecines’ variety of seed handling techniques (Chapman & Russo 2007) may have strong consequences on seed dispersal.

Contrary to their reputation as seed predators (Brockelman, pers. com.), data available in the literature and etho-ecological characteristics of cercopithecine species clearly indicate that semi-terrestrial *Macaca* species may be among the most effective seed dispersers. They are highly frugivorous, use their large cheek pouches extensively, and travel quickly on the ground to reach the food dispersed across their large home range. The study of *Macaca* – the only Cercopithecinae genus in Southeast Asia – could provide a better understanding of the role of cheek-pouched monkeys in tropical rainforest restoration, in an area already deeply threatened by deforestation. Among the seven *Macaca* species found in Thailand (*M. fascicularis, M. mulatta, M. assamensis, M. arctoides, M. silenus, M. nemestrina* and *M. leonina*), *M. actoides, M. nemestrina* and *M. leonina* are the only semi-terrestrial species considered vulnerable by the International Union for the Conservation of Nature (IUCN 2011). Their high terrestriality degree allows them to survive in forests with scarce and scattered food sources. Indeed, terrestrial travel between arboreal food sources is rapid and energy efficient (Rodman 1979) and enables these species to increase their diet diversity by foraging on invertebrates, ground vegetation, fungi and fallen fruits (Caldecott et al. 1996). These macaques, thus, can forage at all rainforest canopy levels, including the ground, in climax evergreen forests as well as secondary forests, making them potentially good seed dispersers.

This study will focus on northern pigtailed macaques' (*Macaca leonina*) role as seed dispersers. Indeed, few studies have been carried out on this species (Choudhury 2003; Davies 1990; Gippoliti 2001; Humphrey & Bain 1990; Khamcha & Sukumal 2009; Kitamura et al. 2002; MacKinnon & MacKinnon 1987; Suzuki et al. 2006; Whitington 1992). Data concerning its ecology and behavior are limited. A better knowledge of *M. leonina* and its disperser role would help plead for its better protection since the species habitat degradation will endanger it in the short term. Northern pigtailed macaques are Cercopithecinae (Fooden 1975) distributed on the Asian mainland north of Peninsular Malaysia (Thailand, Myanmar, Laos, Cambodia, Vietnam, southern China, eastern India, and Bangladesh). Macaques are the most omnivorous of frugivorous primate but still prefer eating fruits when available (*e.g.* Hanya et al. 2003), by no means restricting themselves to the so-called 'primate fruits' – those with large seeds, orange-brown colour, and a protective rind (Corlett 1998). In a study carried out in the Khao Yai National Park, Kitamura *et al.* (2002) estimated that northern pigtailed macaques consumed the fruits of 122 species, more than other frugivores found in the park. They have a large body size (males : 6.2-9.1 kg; females: 4.4-5.7 kg; Rowe & Myers 2011) and form multi-male multi-female troops. Their close relatives, southern pigtailed macaques (*Macaca nemestrina*), form troops ranging from 9 to 81 individuals (Oi 1990).

While following a troop of *M. leonina*, we collected data relating to its seed dispersal activity. Its diet and seed handling have not been extensively documented yet, but the available data (Kitamura et al. 2002) suggest the species might be essential to forest diversity maintenance by dispersing a large number of fruit species, particularly those inaccessible to smaller frugivores due to their large size or their hard protective ring. The goal of this study was to determine the importance of *M. leonina* in primary seed dispersal from two points of view (Schupp 1993; Schupp et al. 2010): (1) quantity, *i.e.* the number of eaten fruit species, their proportion in the diet, the number of feces containing seeds and the number of seeds processed; and (2) quality, *i.e.* the handling techniques used, the seeds' viability and germination success, the habitat type and distances from the parent tree for the deposited seeds, and the dispersal patterns (seeds clumped or scattered).

Methods

Study site

This study was conducted at Khao Yai National Park (KYNP; 2,168 km² 14° 05'–15'N, 101° 05'–50'E). The study site (177 ha), covered by a seasonally wet evergreen forest (Forest Restoration Research Unit 2000), is located around the park Visitor Center at 700-800 m asl, and includes grasslands (4%), shrublands (2%), small tree areas (6%), secondary (14%) and primary (71%) forests, and human settlements (4%). The climate is monsoonal with a wet season (from May to October) and a relatively dry season, which is divided into cool (from November to February) and hot (from March to April) seasons. The average monthly temperature ranges from 19°C (December and January) to 24°C (March and April) and the monthly rainfall averages 69 mm in dry season and 353 mm in wet season (2006-2009).

Study group

We followed one troop of pigtailed macaques (HQ troop) habituated to humans, including 2-3 adult males, 12-13 adult females, 17-23 juveniles and several subadult males. Their home range varied from 32 ha (mean in dry season) to 57 ha (mean in wet season) (Kernel 95%) and included a ranger station and various tourist accommodations. The troop consumed 138 plant species, including 126 fruit, 7 flower, 6 pith, 6 leaf, and 4 shoot species;

human food, including rice, fruits, bread, biscuits, *etc.*; and fungi, ants, termites, spiders, grasshoppers, caterpillars, beetles, and other small animals. However, their diet varied from highly frugivorous during the wet season, to omnivorous during the dry season with an increased part of human food (Chapter 3). Human food was available year-round – the macaques either stole it from houses or trash cans, or received it from tourists. The HQ troop may thus be considered as a semi-provisioned troop.

Data collection

The HQ troop was observed for 1029 hours during a 12 month period divided into three periods for logistic reasons (April - July 2009 [Period 1]: 370 h; December 2009 - March 2010 [Period 2]: 288 h; August - November 2010 [Period 3]: 371 h). Macaques were followed for one of every two or three days, approximately from 0600 h to 1800 h. We used instantaneous samples (Scan sampling: Altmann 1974) of all visible troop members at 30-minute intervals (N = 21,389 observations) to record date and time, number of visible individuals, and the following for each: the age-sex class, activity, height in the canopy, the consumed item, species, consumed part (and age) and, in case of fruit, the processing technique used by the macaque. In this paper, we use the following terminology: "*swallowing*" (W): the seed is put into the mouth, digested and then defecated; "*spitting out*" (S): the seed is put into the mouth and then spat out (often after storage in the cheek pouches); "*dropping*" (D): the seed is cleared from the surrounding pulp, without entering the mouth entirely, and then dropped; and "*crunching*" (C): the seed is put into the mouth and then masticated by the teeth.

During feeding events on fruits, we recorded the behavior of the same ten adult individuals (two males and eight females) during 30-minute continuous focal samplings (Altmann 1974). We noted the species, consumed part (and age), ingested quantity, and handling process used. The fruits were classified as dry, fleshy protected, or fleshy unprotected (Lucas & Corlett 1991). Moreover, we occasionally recorded the time spent in a fruiting patch (*i.e.* discrete site where macaques were feeding and separated from other such sites by at least one tree crown) (Di Fiore 2003).

The troop's locations were based on automatic GPS records taken every 30 minutes. We also recorded the GPS coordinates of the feeding plants and dispersed seeds. Dispersal distances between the dispersed seed and the parent plant were occasionally measured. If the macaque fed on several plants of the same species the dispersal distance could not be determined. Dispersal distances could only be directly measured for spat-out and dropped seeds. The measure of dispersal distances for swallowed seeds relies on an estimation based on knowledge of retention time – information we were not able to obtain during the study.

Habitat types

We recorded the time at every change in habitat type. Within the troop home range, we distinguished two habitat types – human settlements and natural habitats – and five natural habitat sub-types – grassland, shrubland, small trees area, and secondary and primary forest (Chapter 3).

Seed collection

We collected fresh feces found in the forest, weighted them, and noted time of collection, GPS coordinates, and individual origin when possible. We sieved feces through a 0.5 mm nylon mesh to extract the seeds. We counted all the seeds, except those smaller than 2 mm, for which the number was counted in subsamples after having evenly stirred, spread, and divided the feces (Kunz 2008). We collected the spat out and dropped seeds only when spitting and dropping behaviors were observed directly and we noted the time of spitting and dropping, and the individual identity. Defecated, spat-out, and dropped seeds were identified, weighed, and measured (maximum length and width) using callipers. Most *Ficus* species seeds, typically indistinguishable, were not identifiable to the species level. We grouped these species into *Ficus* spp. Seed species that could not be identified were assigned an identification number. We extracted control seeds from intact mature fruits collected in trees foraged by the macaques or on the ground below the tree. We manually removed the pulp (*i.e.* fleshy pericarp) of all fruits and we cleaned the seeds, except for two species where we kept the pulp around 100 seeds to assess the pulp removal effect on seed germination (*i.e.* deinhibtion effect; Baskin & Baskin 2000; Robertson et al. 2006). We classified seeds by length to allow further comparison with other studies (small: maximum length < 5 mm; medium: ≥ 5 mm but < 10 mm; and large: ≥ 10 mm (according to Chapman et al. 2009;

Lambert & Garber 1998; Traveset 1998)). Following Kunz (2008) we considered *M. leonina* as predator for a seed species if (1) unripe fruits were consumed or (2) 100 percent of seeds were crunched (observation in feces or observation of seed consumption rather than fruit pulp).

Viability and germination tests

Before starting germination tests, we performed cut tests (*i.e.* cutting the seed endocarp with a scalpel to expose the seed tissue) on ten seeds of each species for each treatment (defecated, spat-out, dropped or/and control seeds) to control viability. Seeds were scored as viable if firm, moist and if white endosperm was noticed (Ooi et al. 2004). These seeds were not used for germination testing. While aware of the importance of the conditions used to perform the germination test (Robertson et al. 2006), we were unable to set up germination tests in the forest, due to logistical reasons (number of dispersed seeds, time, wildlife passage *etc.*). Germination tests were carried out on as many seeds as possible depending on the species. We used Petri dishes to allow easier comparison with other studies (Traveset et al. 2001). Defecated, spat-out, dropped, and control seeds were laid on a damp filter paper layer in Petri dishes to determine the effect of macaques' seed processing techniques on seed germinability. Filter papers were regularly moistened during germination tests to avoid seed desiccation. Petri dishes were labelled and piled on shaded shelves which were protected from rain and predators. The germinated seed number was checked every week. Radicle emergence was used as germination index and germinating seeds were removed from the Petri dishes after counting. Each un-germinated seed stayed in the germination test for six months. At the end of the test, the remaining un-germinated seeds' viability was checked to determine if seeds were dead or dormant. Only species with at least four Petri dishes per treatment (with at least four seeds each) were taken into account in the analysis.

Food list

We included as food species every plant species present in scan, fecal, spit-out and drop samples, and every plant consumed between scan samples. Species found only once in feces were not taken into account to prevent biases due to unintentional ingestion. We assessed plant species importance in the diet according to the quantity and the duration of the consumption observed for each species (Doran et al. 2002). "Large quantity" means occurring in at least 50 percent of fecal samples during at least one month. "Long duration" means at least six months (50% of months). Type I defines seed species observed in large quantity and for long duration. Type II defines seed species observed in small quantity and for long duration. Type III defines seed species observed in large quantity for short duration. Type IV defines plant species observed during at least 5 percent of scan sampling observations.

Statistical analysis

We performed two-tailed statistical tests with Statistica 9.0 (α level: 0.05). We compared the seed processing effect on seed median length of germination time (MLGT), germination percentage and viability percentage at the end of the test with the Mann-Whitney *U*-test between processed and control seeds, and between control with pulp and without pulp for each tested species. To highlight the seasonal variation in dietary diversity, we calculated a Shannon diversity index (H') for each study month.

Results

Diet

The studied macaques showed a clear preference for ripe fruits (92%) compared to unripe (8%) and old (<1%) fruits regardless of plant species (N = 731 scan sampling observations). They ate fruits of various plant forms: herbs, shrubs, small to tall trees, epiphytes, and lianas. During scan sampling, 1818 feeding events were recorded, from which we identified 53 fruit, 4 flower, 3 pith, and 3 shoot species, with an average of 8.8 ± 4.4 species per month. According to scan sampling, the troop consumed an average of 7.5 ± 4.7 fruit species per month and 5.0 ± 3.3 fruit species per day, and the average Shannon diversity index was of 1.67 ± 0.60 (Figure 2.1). All 15 plant species considered as important species in the diet were consumed at least for their fruits (Table 2.1). Subsequent observations showed that *Bridelia insulana* and *Cinnamomum iners* could also be considered as important species (Type II).

Table 2.1. Important plant species in the troop's diet. Type I: seed species observed during at least 6 months in large quantity. Type II: seed species observed during at least 6 months in small quantity. Type III: seed species observed during less than 6 months but in large quantity. Type IV: plant species observed during at least 5 percent of observations during scan sampling. * Predated species. Fr = fruit, Fl = flower, Pi = pith, Sho = shoot, W = swallow, C = crunch, S = spit out, D = drop, nd = not determined.

Species	Family	Life form	Part consumed	Process	Seed length (mm)
Type I					
Species n°198	Theaceae	nd	Fr	W	2.67
Ficus spp.	Moraceae	Tree/Liana	Fr	W	1.43
Solanum melongena	Solanaceae	Shrub	Fr	W	2.43
Type II					
Species n°90	nd	nd	Fr	W, C	6.68
Type III					
Anthocephalus chinensis	Rubiaceae	Tall tree	Fr	W	0.50
Baccaurea ramiflora	Euphorbiaceae	Small tree	Fr	W, S, D	11.50
Diplectria barbata	Melastomataceae	Liana	Fr	W	0.81
Eurya nitida	Theaceae	Small tree	Fr, Fl	W	1.68
Melastoma malabathricum	Melastomataceae	Shrub	Fr	W	0.50
Toddalia asiatica	Rutaceae	Liana	Fr	W	5.40
Type IV					
Alpinia malaccensis	Zingiberaceae	Herb	Fr, Pi, Sho	W	7.11
*Daemonorops jenkinsiana**	Palmae	Liana	Fr, Pi, Sho	C	14.92
*Diospyros glandulosa**	Ebenaceae	Small tree	Fr	C	12.13
Macaranga spp.*	Euphorbiaceae	Medium/tall tree	Fr	C	2.54
Machilus odoratissima	Lauraceae	Medium tree	Fr	S	7.19

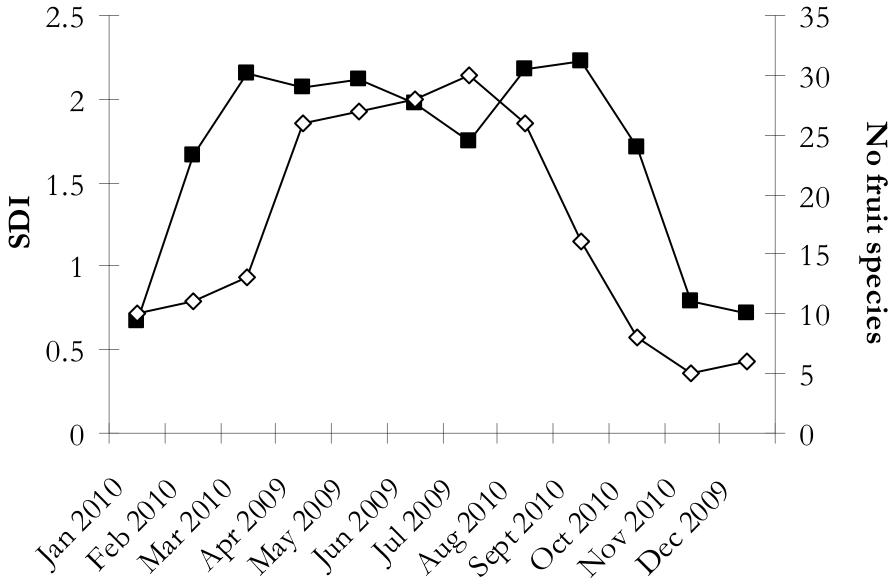


Figure 2.1. Monthly numbers of fruit species consumed (open circles) and dietary diversity of the study troop calculated from the Shannon diversity index (SDI; black squares).

Seed processing

Macaques used four seed processing techniques: "swallow" (93 species), "spit out" (36 species), "drop" (18 species) and "crunch" (48 species). They could use several techniques for a same species. Indeed, they used two techniques for 9 percent of fruit species and three techniques for 1 percent of them. Processed seeds were dispersed in all natural habitat types (grasslands, shrublands, small tree areas, secondary and primary forests).

Out of 335 fecal samples collected (Table 2.2), 89 percent contained seeds. Collected feces weighted 15.01 ± 6.19 g on average (*N* = 273) and each 15g fecal sample contained an average of 1.9 ± 1.4 species (range = 1-9). We found an average of 13.2 ± 7.6 plant species in feces per month. Seeds contained in the mainly intact feces were clumped and were as large as 20 mm (*Garcinia benthamii*; Guttiferae). We found in feces only 36 percent of the species seen consumed during following (*N* = 84 species). This weak overlap between data collection techniques shows their complementarity for the diet description.

An average of 3.3 ± 3.6 species per month was spat out (Table 2.2). Occasional measures showed macaques could keep seeds into their cheek pouches up to 45 minutes before spitting them out, allowing the long dispersal distances observed for several seed species (Table 2.3). Thus, if seeds were spat out when macaques moved, they could be widely scattered. However, we observed many spat out seeds deposited under the parent tree. An average of 1.6 ± 2.6 species per month was dropped (Table 2.2).

Seeds processed without visible damage (*i.e.* not crunched) represented 69 percent of the total number of seeds swallowed, spat out, dropped and crunched. Macaques were considered as predators for 38 seed species, 22 coming from dry fruits (mainly Leguminosae and Fagaceae) and 5 from Palmae fruits. For three species (*Licuala spinosa*, *Polyalthia evecta*, *Psychotria ophioxyloides*), predation is due to the consumption of immature fruits (8% of feeding observations; *N* = 1,818). Only three of these predated species were considered important species in the diet (Type IV; Table 2.1). After removing the predated species from the analysis, the percentage of seeds processed without visible damage reached 97 percent.

The technique used by macaques to process seeds is influenced by seed size (Figure 2.2). The frequency of ingestion varied according to fruit species (*N* = 21) from 1 to 99 fruits per minute. The number of individuals feeding in the same patch varied from one member to all troop members. The duration of a feeding visit to a fruiting patch varied from a few seconds to three hours.

Table 2.2. Main species found in fecal samples (15g each), spat-out and drops.

Species	Family	Percent of seeds	No seeds/sample ± SD (No samples)
Fecal samples (62 fruits species)			2053.6 ± 3382.5 (335)
Large-seeded species (67 samples; 321 seeds; 11 species)			
Baccaurea ramiflora	Euphorbiaceae	67%	5.4 ± 6.0 (38)
Garcinia benthamii	Guttiferae	13%	4.1 ± 3.6 (10)
Gnetum macrostachyum	Gnetaceae	10%	2.6 ± 2.6 (11)
Medium-seeded species (58 samples; 1930 seeds; 18 species)			
Toddalia asiatica	Rutaceae	95%	54.1 ± 71.7 (31)
Small-seeded species (286 samples; 667,834 seeds; 33 species)			
Diplectria barbata	Melastomataceae	43%	3777.5 ± 4778.0 (72)
Ficus spp.	Moraceae	27%	684.2 ± 1615.2 (248)
Melastoma malabathricum	Melastomataceae	23%	2506.9 ± 3370.3 (59)

Spat-out (30 fruit species)		
Large-seeded species (798 seeds; 17 species)		
Ziziphus attopensis	Rhamnaceae	17%
Baccaurea ramiflora	Euphorbiaceae	16%
Gnetum montanum	Gnetaceae	14%
Syzygium cumini	Myrtaceae	10%
Medium-seeded species (1116 seeds; 10 species)		
Syzygium syzygioides	Myrtaceae	23%
Syzygium sp. n°152	Myrtaceae	16%
Balakata baccata	Euphorbiaceae	15%
Machilus odoratissima	Lauraceae	14%
Small-seeded species (2763 seeds; 3 species)		
Ficus spp.	Moraceae	93%
Eurya nitida	Theaceae	4%
Syzygium cinereum	Myrtaceae	3%
Drops (17 fruits species)		
Large-seeded species (506 seeds; 13 species)		
Baccaurea ramiflora	Euphorbiaceae	31%
Antiaris toxicaria	Moraceae	26%
Mangifera indica	Anacardiaceae	18%
Areca triandra	Palmae	7%
Medium-seeded species (248 seeds; 4 species)		
Species n°14	Unknown	64%
Artocarpus lakoocha	Moraceae	26%
Michelia baillonii	Magnoliaceae	9%

Table 2.3. Maximum dispersal distance computed for several seed species processed by the study troop.

Species	Mean seed dimensions (mm)	Dispersal distance (m)	Process
Bridelia insulana	9.61 x 5.65	141	Spit out
Cinnamomum iners	10.95 x 7.26	262	Spit out
Machilus odoratissima	7.19 x 7.19	240	Spit out
Mangifera indica	57.67 x 33.43	130	Drop
Syzygium cinereum	4.05 x 3.68	265	Spit out
Syzygium cumini	13.37 x 8.04	147	Spit out

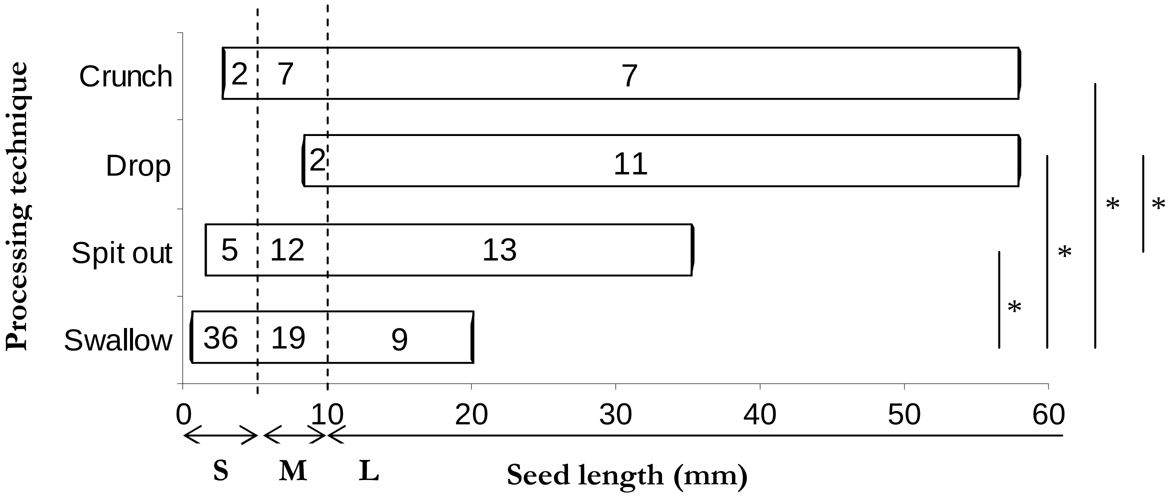


Figure 2.2. Seed size intervals concerned by each processing technique used by the study troop. In each interval, the number of small- (S), medium- (M), and large-seeded (L) species swallowed, spat out, dropped, and crunched by the study troop is indicated (*N* = 86 seed species). Mann–Whitney *U*-Tests: * $P < 0.001$.

Seed processing effect on seed germination and viability

Due to reduced sample size for many species, germination and viability analyses were performed for only 21 species. Moreover, four species were removed for the MLGT analysis. Indeed, for two species, no seed germinated after six months; for two other species, only one or two seeds germinated for one treatment, which gave uncertain estimates of MLGT. For swallowed and spat-out seeds, results show a mainly neutral effect on seed germination and viability (Table 2.4). Indeed, there was no significant difference between processed and control seeds for (1) 9 species out of 17 tested for differences in MLGT, (2) 17 species out of 21 tested for differences in germination percentages, and (3) 15 species out of 21 tested for differences in viability percentages. For *Baccaurea ramiflora*, this neutral effect only concerns spat-out seeds.

Pulp effect on seed germination and viability

Due to reduced sample size, analyses on pulp effect were performed for only two species (*Baccaurea ramiflora* and *Syzygium cinereum*). The pulp had a significant negative effect on MLGT, germination percentage and viability percentage for both species (Table 2.4). For many other species, we observed fast attack by fungi on uneaten fruits fallen to the ground.

Table 2.4. Mean ± SD of median length of germination time (MLGT), germination percentage and final viability percentage of control seeds (Control) and treatment seeds (Treatment), *i.e.* seeds swallowed (W) or spat-out (S) or control seeds with pulp (Cpp). Note that *Baccaurea ramiflora* is tested with S, W and Cpp and that *Syzygium cinereum* is tested with S and Cpp. Significant differences between control and treatment seeds are in bold ($P < 0.05$). The number of seed tested *(N)* is *italize*; nd = not determined.

	MLGT (days)		**Germination (%)**		**Viability (%)**	
Species	**Control**	**Treatment**	**Control**	**Treatment**	**Control**	**Treatment**
Alpinia malaccensis (W)	156 ± 0 *(37)*	170 ± 53 *(24)*	10 ± 19 *(37)*	17 ± 7 *(24)*	100 ± 0 *(37)*	100 ± 0 *(24)*
Alphonsea boniana (S)	nd	nd	7 ± 10 *(23)*	10 ± 22 *(21)*	43 ± 27 *(23)*	45 ± 41 *(21)*
Anthocephalus chinensis (W)	134 ± 91 *(90)*	110 ± 88 *(51)*	**54 ± 6** *(90)*	**15 ± 32** *(51)*	**97 ± 7** *(90)*	**79 ± 6** *(51)*
Artocarpus lakoocha (S)	60 ± 8 *(52)*	55 ± 11 *(18)*	79 ± 23 *(52)*	79 ± 25 *(18)*	79 ± 23 *(52)*	79 ± 25 *(18)*
Baccaurea ramiflora (W)	**8 ± 0** *(100)*	**12 ± 5** *(97)*	**100 ± 0** *(100)*	**92 ± 7** *(97)*	**100 ± 0** *(100)*	**92 ± 7** *(97)*
Baccaurea ramiflora (S)	8 ± 0 *(100)*	8 ± 0 *(100)*	100 ± 0 *(100)*	100 ± 0 *(100)*	100 ± 0 *(100)*	100 ± 0 *(100)*
Baccaurea ramiflora (Cpp)	**8 ± 0** *(100)*	**34 ± 10** *(100)*	**100 ± 0** *(100)*	**75 ± 18** *(100)*	**100 ± 0** *(100)*	**75 ± 18** *(100)*
Balakata baccata (S)	nd	nd	0 ± 0 *(16)*	0 ± 0 *(19)*	56 ± 13 *(16)*	64 ± 8 *(19)*
Bridelia insulana (S)	14 ± 5 *(100)*	17 ± 3 *(99)*	93 ± 9 *(100)*	85 ± 11 *(99)*	93 ± 9 *(100)*	85 ± 11 *(99)*
Diplectia barbata (W)	25 ± 7 *(195)*	19 ± 0 *(192)*	12 ± 11 *(195)*	9 ± 8 *(192)*	100 ± 0 *(195)*	100 ± 0 *(192)*
Eurya nitida (W)	**148 ± 87** *(94)*	**252 ± 16** *(96)*	**60 ± 60** *(94)*	**15 ± 15** *(96)*	95 ± 95 *(94)*	96 ± 96 *(96)*
Ficus ischnopoda (W)	12 ± 0 *(150)*	14 ± 10 *(117)*	93 ± 7 *(150)*	66 ± 35 *(117)*	93 ± 7 *(150)*	88 ± 14 *(117)*
Ficus microcarpa (W)	**11 ± 0** *(52)*	**17 ± 0** *(100)*	89 ± 10 *(52)*	96 ± 4 *(100)*	89 ± 10 *(52)*	96 ± 4 *(100)*
Ficus sagittata (W)	**17 ± 2** *(45)*	**13 ± 3** *(200)*	83 ± 24 *(45)*	99 ± 2 *(200)*	83 ± 24 *(45)*	99 ± 2 *(200)*
Ficus virens (W)	**9 ± 1** *(97)*	**13 ± 0** *(200)*	80 ± 12 *(97)*	88 ± 8 *(200)*	84 ± 14 *(97)*	94 ± 6 *(200)*
Gnetum montanum (S)	nd	nd	0 ± 0 (24)	0 ± 0 (100)	**0 ± 0** (24)	**35 ± 20** (100)

Litsea monopetala (S)	**92 ± 0** *(20)*	**52 ± 35** *(20)*	**75 ± 0** *(20)*	**25 ± 0** *(20)*	**75 ± 0** *(20)*	**25 ± 0** *(20)*
Melastoma malabathricum (W)	19 ± 5 *(200)*	17 ± 4 *(200)*	**40 ± 11** *(200)*	**12 ± 9** *(200)*	**40 ± 11** *(200)*	**12 ± 9** *(200)*
Nauclea orientalis (W)	**12 ± 71** *(95)*	**119 ± 0** *(91)*	10 ± 10 *(95)*	20 ± 12 *(91)*	**10 ± 19** *(95)*	**40 ± 12** *(91)*
Syzygium cinereum (S)	8 ± 4 *(100)*	6 ± 1 *(102)*	87 ± 11 *(100)*	95 ± 7 *(102)*	87 ± 11 *(100)*	95 ± 7 *(102)*
Syzygium cinereum (Cpp)	**8 ± 4** *(100)*	**22 ± 6** *(100)*	**87 ± 11** *(100)*	**36 ± 17** *(100)*	**87 ± 11** *(100)*	**36 ± 17** *(100)*
Syzygium sp. n°152 (S)	**6 ± 5** *(12)*	**1 ± 0** *(10)*	88 ± 18 *(12)*	90 ± 12 *(10)*	88 ± 18 *(12)*	90 ± 12 *(10)*
Toddalia asiatica (W)	nd	nd	2 ± 4 *(56)*	4 ± 6 *(146)*	66 ± 20 *(56)*	63 ± 14 *(146)*
Species n° 192 (W)	125 ± 17 *(190)*	122 ± 20 *(100)*	20 ± 11 *(190)*	6 ± 39 *(100)*	**95 ± 19** *(190)*	**45 ± 5** *(100)*

Discussion

The northern pigtailed macaques observed in this study satisfy most requirements defining effective seed dispersers in both quantitative and qualitative terms (Schupp 1993; Schupp et al. 2010): (1) they dispersed many seeds of many species, (2) in every natural habitat type, (3) their effect on seed germination and viability seemed to be neutral for most of the species, and (4) they used various seed processing techniques and dispersed seeds of small-, medium- and large-seeded species. Moreover, we also knew that (5) they had a large home range and traveled long distances in one day (Chapter 3).

Seed dispersal quantity

Several factors affect seed dispersal quantity (Schupp 1993; Schupp et al. 2010): (1) the number of times a disperser species visits a particular plant species, which is influenced by the disperser species abundance, diet, and reliability of its visits to this plant species, and (2) the number of seeds dispersed per visit, which is influenced by the number of processed seeds, and their probability to be dispersed. *Macaca leonina* has been very little studied, so data on its density and abundance in KYNP are unfortunately lacking. Our results showed that northern pigtailed macaques were important dispersers as they had a highly diversified diet including at least 126 fruit species (Andresen 2002; Poulsen et al. 2001). However, like many animal species, only some plant species made up the greatest part of their monthly diet (Milton 2000). A previous study (Chapter 3) described *Macaca leonina* as a "traplining" species usually visiting the same patches of fruiting trees for several days or even weeks. This conclusion highlights the reliability of this disperser throughout a significant part of the fruiting period for some plant species. We showed that the troop could process many seeds per visit: it included between 32 and 39 individuals, with up to 39 individuals in the same fruiting patch at a given time, each consuming up to 99 fruits per minute, and staying in the patch for up to three hours. The probability that seeds processed by macaques were dispersed is strongly dependent on the plant species. If the seed is among the 38 seed species predated by macaques, then the probability is close to zero. However, if the seed is among the 88 other species, the probability is very high (97 %) and can be compared to the probabilities seen in other sympatric dispersers such as gibbons (90%) and hornbills (100%) (Savini & Kanwatanakid-Savini 2011).

Seed dispersal quality

According to Schupp (1993), seed dispersal quality depends on the seed treatment quality in the mouth and gut, and on the seed deposition quality. As seen above, a significant seed species proportion is predated by macaques, but only three of them are either eaten in large quantity or for long duration. When seeds were not crunched, processing by macaques neither altered the germination and viability percentages nor the MLGT for most plant species, indicating a neutral seed treatment in the mouth and gut for these species.

The fact that macaques decrease seed germination percentage, and delay germination for some species, is interesting, as few studies have already shown this in primates (Chapman 1989; Estrada & Coates-Estrada 1984; Otani 2004). Conversely, few studies have shown a shorter MLGT in processed seeds (Chapman et al. 2009; Righini et al. 2004; Wehncke & Dalling 2005; Wrangham et al. 1994). But, the consequences of an increase or a decrease in MLGT are difficult to predict (Valenta & Fedigan 2009; Verdú & Traveset 2005). Thus, we did not use the MLGT to estimate the global effect of processing by macaques. In summary, this global effect (*i.e.* germination percentage and viability percentage) was neutral for 13 species, positive for 2 species, negative for 5 species, and neutral (spat-out seeds) and negative (swallowed seeds) for 1 species. This mainly neutral effect has also been reported in many primate studies, *e.g.* for gibbons (McConkey 2000) or tamarins (Knogge et al. 2003).

Concerning viability, many studies did not show the percentage of viable seeds after test. However, these data are necessary to complete the results obtained with the germination tests by making the difference between dead and dormant seeds (Robertson et al. 2006). Indeed, many un-germinated seeds were still viable and could still germinate if exposed to appropriate conditions.

Our results confirmed that pulp removal increased seed viability and germination. However, our tests were performed in experimental conditions only, and Robertson *et al.* (2006) have shown, for seeds in intact fruits, a much lower germination percentages in Petri dishes than in the field. Germination tests in the field should be performed to confirm the effect of pulp removal.

Macaques had a larger home range than sympatric primate species, and traveled more than 1500 m, on average, each day (Chapter 3), which increased the probability that seeds were dispersed far from the parent plant (> 100 m; Cain et al. 2000; Russo et al. 2006) . Moreover, they used every natural habitat type and three different seed dispersal techniques, which increased the probability that the seeds were dispersed in a suitable way and in a suitable place, all the more reason that the places' suitability is spatially and temporally unpredictable and often context-dependent (Schupp 1988, 1993, 2007). Defecation of many seeds in clumps should not be a problem for most species given that seed dispersal is often a multi-step process. After dispersal by primary dispersers at some distance from parent plants, secondary dispersers will then scatter seeds and move them in suitable places (Schupp et al. 2010).

Finally, our study supports the prediction that *M. leonina* effectively disperses the seeds of many plant species despite the possible negative effect of seed clumping in feces and the mostly neutral effect of seed processing by macaques on seed germination and viability. Indeed, compared to non-dispersed seeds, the advantages of seed dispersal by *M. leonine,* lie more in (1) an increased probability of deposition in a suitable place and pattern due to the use of multiple seed handling techniques, (2) an increased dispersal distance, and (3) an increased germination probability due to pulp removal. This third point may be confirmed by referring to Samuels and Levey (2005) who stated that when IF < ME = GP (where IF = germination of seeds from intact fruits, ME = germination of manually extracted seeds, and GP = germination of gut passed seeds), then the animal is only needed to separate seeds from fruit pulp.

Implications for conservation: their role in forest succession

As a prevalent and effective disperser, *M. leonina* could have a great impact on rainforest maintenance and on degraded area regeneration. Ideally, seeds dispersed into degraded areas would include early-, mid-, and late-successional species (Duncan & Chapman 2002). We have shown that they dispersed seeds of every life form, in every natural habitat type, even grasslands. The characteristics of *M. leonina* could thus be used in management plans for forest restoration and regeneration, in a similar way seed dispersal by birds has been used (Scott *et al.* 2000). Northern pigtailed macaques could also disperse species of economic interest, such as *Balakata baccata* (Euphorbiaceae) used for timber, and for its bark in traditional medicine (Forest Restoration Research Unit 2006).

Directions for future research

The study of seed dispersal by semi-provisioned animals is necessary. Given that most degraded areas are human dominated landscapes (Corlett 1998; Kitamura et al. 2002), we have to know if seed dispersers remain effective even in presence of humans. However, we cannot generalize directly our results to other troops, and further studies in un-provisioned conditions will be necessary. By comparing our results with those of Kitamura *et al.* (2002) about unprovisioned macaques, we highlighted dietary and processing variations between macaques troops. Indeed, the dietary overlap between the HQ troop and the macaques studied by Kitamura *et al.* (2002) was of 47 plant species only. This finding shows that northern pigtailed macaques are able to live in various environments, with different resources, by adapting their diet according to the available plant species, as already shown in other primate species (Ganas et al. 2004). Moreover, seed treatment seemed to vary between troops, particularly for some plant species reported as dispersed in Kitamura *et al.* (2002) but reported as predated in our study, and *vice versa*. The difference in resources available in each environment may induce various kinds of behavior (to crunch the seed or to reject it) according to the needs in some nutrients. All these potential variations indicate the necessity to study other troops of northern pigtailed macaques, particularly troops living in more remote areas, without access to human food. However, we can already predict that un-provisioned troops should be as effective, if not more effective, dispersers than HQ. Because the home range of semi-provisioned troops is generally smaller than that of un-provisioned troops, we can suppose that other macaques troops' home range at KYNP should be larger, mainly in wet season (Altmann & Muruthi 1988), increasing the probability of seed dispersal far from the parent plant. Moreover, un-provisioned troops should eat more fruits (and maybe more fruit species) and less human food, and should disperse more seeds than the HQ troop. Finally, in this study we focused only on the first step of the seed dispersal process, *i.e.* from fruit removal to seed germination (in experimental conditions). The study of later life stages of the dispersed seeds, including post-dispersal predation and secondary dispersal, would be necessary to confirm the effectiveness of *M. leonina* in seed dispersal (Schupp et al. 2010).

Acknowledgments

We thank the Department of National Parks, Wildlife and Plant Conservation and the National Research Council of Thailand for granting research permission, and the superintendent of Khao Yai National Park for his hospitality. We thank Alice Latinne for her valuable advices, and Lee Olsen for editing the English. This study was carried out with the financial support from the University of Liège, Belgium (A.A), and of the Biodiversity Research and Training Program, Thailand (Grant No. BRT R_349007) (T.S. and M-C.H.).

Literature cited

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, 49, 227-267.

Altmann, J. & Muruthi, P. 1988. Differences in daily life between semiprovisioned and wild-feeding baboons. *American Journal of Primatology*, 15, 213-221.

Andresen, E. 2002. Primary seed dispersal by red howler monkeys and the effect of defecation patterns on the fate of dispersed seeds. *Biotropica*, 34, 261-272.

Baskin, C. C. & Baskin, J. M. 2000. *Seeds: ecology, biogeography, and evolution of dormancy and germination*. London: Academic Press.

Cain, M. L., Milligan, B. G. & Strand, A. E. 2000. Long-distance seed dispersal in plant populations *American Journal of Botany*, 87, 1217-1227.

Caldecott, J. O., Feistner, A. T. C. & Gadsby, E. L. 1996. A comparison of ecological strategies of pig-tailed macaques, mandrills and drills. In: *Evolution and ecology of macaque societies* (Ed. by Fa, J. E. & Lindburg, D. G.), pp. 73-94. Cambridge Cambridge University Press.

Chapman, C. A. 1989. Primate seed dispersal: The fate of dispersed seeds. *Biotropica*, 21, 148-154.

Chapman, C. A. & Onderdonk, D. A. 1998. Forests without primates: Primate/plant codependency. *American Journal of Primatology*, 45, 127-141.

Chapman, C. A. & Russo, S. E. 2007. Primate seed dispersal: Linking behavioral ecology with forest community structure. In: *Primates in perspective* (Ed. by Campbell, C. J., Fuentes, A. F., MacKinnon, K. C., Panger, M. & Bearder, S.), pp. 510-525. Oxford: Oxford University Press.

Chapman, H. M., Goldson, S. L. & Beck, J. 2009. Postdispersal removal and germination of seed dispersed by *Cercopithecus nictitans* in a West African montane forest. *Folia primatologica*, 81, 41-50.

Chaves, Ó. M., Stoner, K. E., Arroyo-Rodríguez, V. & Estrada, A. 2011. Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rain forests in southern Mexico. *International Journal of Primatology*, 32, 177-192.

Choudhury, A. 2003. The pig-tailed macaque *Macaca nemestrina* in India - Status and conservation. *Primate Conservation*, 19, 91-98.

Cordeiro, N. J. & Howe, H. F. 2001. Low recruitment of trees dispersed by animals in African forest fragments. *Conservation Biology*, 15, 1733-1741.

Corlett, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews*, 73, 413-448.

Corlett, R. T. & Hau, B. C. H. 2000. Seed dispersal and forest restoration. In: *Forest restoration for wildlife conservation* (Ed. by Elliott, S., Kerby, J., Blakesley, D., Hardwick, K., Woods, K. & Anusarnsunthorn, V.), pp. 317-325. Chiang Mai University, Thailand: International Tropical Timber Organisation and The Forest Restoration Research Unit.

Corlett, R. T. & Lucas, P. W. 1990. Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*). *Oecologia*, 82, 166-171.

Davies, R. G. 1990. Sighting of a clouded leopard (*Neofelis nebulosa*) in a troop of pigtail macaques (*Macaca nemestrina*) in Khao Yai National Park, Thailand. *Natural History Bulletin of the Siam Society*, 28, 95-96.

Dew, J. L. & Wright, P. 1998. Frugivory and seed dispersal by four species of primates in Madagascar's Eastern rain forest. *Biotropica*, 30, 425-437.

Di Fiore, A. 2003. Ranging behavior and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Yasuní National Park, Ecuador. *American Journal of Primatology*, 59, 47-66.

Doran, D. M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P. & Shah, N. 2002. Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling method. *American Journal of Primatology*, 58, 91-116.

Duncan, R. S. & Chapman, C. A. 2002. Limitations of animal seed dispersal for enhancing forest succession on degraded lands. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 437-450. New York: CAB International.

Estrada, A. & Coates-Estrada, R. 1984. Fruit eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxlas, Mexico. *American Journal of Primatology*, 6, 77-91.

Fooden, J. 1975. Taxonomy and evolution of liontail and pigtail macaques (Primates: Cercopithecidae). *Fieldiana: Zoology*, 67, 1-168.

Forest Restoration Research Unit. 2000. Tree seeds and seedlings for restoring forests in Northern Thailand. Biology Department, Science Faculty, Chiang Mai University, Thailand.

Forest Restoration Research Unit. 2006. *How to plant a forest: the principles and practice of restoring tropical forests*. Biology Department, Science Faculty, Chiang Mai University, Thailand.

Forest Restoration Research Unit. 2008. *Research for restoring tropical forest ecosystems: A practical guide*. Biology Department, Science Faculty, Chiang Mai University, Thailand.

Ganas, J., Robbins, M. M., Nkurunungi, J. B., Kaplin, B. A. & McNeilage, A. 2004. Dietary variability of mountain gorillas in Bwindi Impenetrable National park, Uganda. *International Journal of Primatology*, 25, 1043-1072.

Garber, P. A. & Lambert, J. E. 1998. Introduction to primate seed dispersal. Primates as seed dispersers: ecological processes and directions for future research. *American Journal of Primatology*, 45, 3-8.

Gippoliti, S. 2001. Notes on the taxonomy of *Macaca nemestrina leonina* Blyth, 1863 (Primates: Cercopithecidae). *Hystrix Italian Journal of Mammalogy*, 12, 51-54.

Hanya, G., Noma, N. & Agetsuma, N. 2003. Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima. *Primates*, 44, 51-59.

Humphrey, S. R. & Bain, J. R. 1990. *Endangered animals of Thailand*. Gainesville, Florida: Sandhill Cran Press.

IUCN. 2011. IUCN Red List of Threatened Species. Version 2011.1. http://www.iucnredlist.org Downloaded on 26/10/2011.

Khamcha, D. & Sukumal, N. 2009. *Python molurus* predation on a *Macaca nemestrina* in Khao Yai National Park, Thailand. *Hamadryad*, 34, 176-178.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T. & Noma, N. 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133, 559-572.

Knogge, C., Herrera, E. R. T. & Heymann, E. W. 2003. Effects of passage through tamarin guts on the germination potential of dispersed seeds. *International Journal of Primatology*, 24, 1121-1128.

Kunz, B. K. 2008. Frugivory and seed dispersal: ecological interactions between baboons, plants, and dung beetles in the savanna-forest mosaic of West Africa. PhD, University of Würzburg.

Lambert, J. E. 2001. Red-tailed guenons (*Cercopithecus ascanius*) and strychnos mitis: evidence for plant benefits beyond seed dispersal. *International Journal of Primatology*, 22, 189-201.

Lambert, J. E. & Garber, P. A. 1998. Evolutionary and ecological implications of primate seed dispersal. *American Journal of Primatology*, 45, 9-28.

Laurance, W. F. 2007. Forest destruction in tropical Asia. *Current Science*, 93, 1544-1550.

Lucas, P. W. & Corlett, R. T. 1991. Relationship between the diet of *Macaca fascicularis* and forest phenology. *Folia primatologica*, 57, 201-215.

MacKinnon, J. R. & MacKinnon, K. S. 1987. Conservation status of the primates of the Indo-Chinese subregion. *Primate Conservation*, 8, 187-195.

McConkey, K. R. 2000. Primary seed shadow generated by gibbons in the rain forests of Barito Ulu, central Borneo. *American Journal of Primatology*, 52, 13-29.

Milton, K. 2000. Quo vadis? Tactics of food search and group movement in primates and other animals. In: *On the move: How and why animals travel in groups* (Ed. by Boinski, S. & Garber, P. A.), pp. 375-417. Chicago and London: The University of Chicago press.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858.

Oi, T. 1990. Population organization of wild pig-tailed macaques (*Macaca nemestrina nemestrina*) in West Sumatra. *Primates*, 31, 15-31.

Ooi, M., Auld, T. & Whelan, R. 2004. Comparison of the cut and tetrazolium tests for assessing seed viability: a study using Australian native Leucopogon species. *Ecological management and restoration*, 5, 141-143.

Otani, T. 2004. Effects of macaque ingestion on seed destruction and germination of a fleshy-fruited tree, *Eurya emarginata*. *Ecological Research*, 19, 495-501.

Parrotta, J. A. 2000. Catalysing natural forest restoration on degraded tropical landscapes. In: *Forest restoration for wildlife conservation* (Ed. by Elliott, S., Kerby, J., Blakesley, D., Hardwick, K., Woods, K. & Anusarnsunthorn, V.). Chiang Mai University, Thailand: International Tropical Timber Organisation and The Forest Restoration Research Unit.

Poulsen, J. R., Clark, C. J. & Smith, T. B. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology*, 17, 787-808.

Pringle, E. G., Álvarez-Loayza, P. & Terborgh, J. 2007. Seed characteristics and susceptibility to pathogen attack in tree seeds of the Peruvian Amazon. *Plant Ecology*, 193, 211-222.

Righini, N., Serio-Silva, J. C., Rico-Gray, V. & Martínez-Mota, R. 2004. Effect of different primate species on germination of *Ficus* (*Urostigma*) seeds. *Zoo Biology*, 23, 273-278.

Robertson, A. W., Trass, A., Ladley, J. J. & Kelly, D. 2006. Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. *Functional Ecology*, 20, 58-66.

Rodman, P. S. 1979. Skeletal differentiation of *Macaca fascicularis* and *Macaca nemestrina* in relation to arboreal and terrestrial quadrupedalism. *American Journal of Physical Anthropology*, 51, 51-62.

Rowe, N. & Myers, M. 2011. All the World's Primates. www.alltheworldsprimates.org. Primate Conservation Inc. Charlestown RI. Downloaded on 10/10/2011. Charlestown RI.

Russo, S. E., Portnoy, S. & Augspurger, C. K. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology*, 87, 3160-3174.

Samuels, I. A. & Levey, D. J. 2005. Effects of gut passage on seed germination: do experiments answer the questions they ask? *Functional Ecology*, 19, 365-368.

Savini, T. & Kanwatanakid-Savini, C. 2011. Feeding overlap and seed dispersal efficiency between sympatric hornbills and gibbons in Thailand. *The Raffles Bulletin of Zoology*, 24, 115-122.

Schupp, E. W. 1988. Factor affecting post-dispersal seed survival in a tropical forest. *Oecologia*, 76, 525-530.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*, 107/108, 15-29.

Schupp, E. W. 2007. The suitability of a site for seed dispersal is context-dependent. In: *Seed dispersal: theory and its application in a changing world* (Ed. by Dennis, A. J., Schupp, E. W., Green, R. A. & Westcott, D. A.), pp. 445-462. Wallingford, UK: CAB International.

Schupp, E. W., Jordano, P. & Gómez, J. M. 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist*, 188, 333-353.

Scott, R., Pattanakaew, P., Maxwell, J. F., Elliott, S. & Gale, G. 2000. The effect of artificial perches and local vegetation on bird-dispersed seed deposition into regenerating sites. In: *Forest restoration for wildlife conservation* (Ed. by Elliott, S., Kerby, J., Blakesley, D., Hardwick, K., Woods, K. & Anusarnsunthorn, V.), pp. 326-337. Chiang Mai University, Thailand: International Tropical Timber Organisation and The Forest Restoration Research Unit.

Sodhi, N. S., Koh, L. P., Brook, B. W. & Ng, P. K. L. 2004. Southeast Asian biodiversity: an impending disaster. *Trends in Ecology and Evolution*, 19, 654-660.

Suzuki, S., Kitamura, S., Kon, M., Poonswad, P., Chuailua, P., Plongmai, K., Yumoto, T., Noma, N., Maruhashi, T. & Wohandee, P. 2006. Foraging activity patterns of frugivorous or omnivorous animals on the forest floor of a tropical seasonal forest in Thailand, with reference to seasonal changes. *Natural History Bulletin of the Siam Society*, 54, 177-194.

Tang, Z.-H., Cao, M., Sheng, L.-X., Ma, X.-F., Walsh, A. & Zhang, S.-Y. 2008. Seed dispersal of *Morus macroura* (Moraceae) by two frugivorous bats in Xishuangbanna, SW China. *Biotropica*, 40, 127-131.

Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics*, 1/2, 151-190.

Traveset, A., Riera, N. & Mas, R. E. 2001. Passage through bird guts causes interspecific differences in seed germination characteristics. *Functional Ecology*, 15, 669-675.

Traveset, A. & Verdú, M. 2002. A meta-analysis of the effect of gut treatment on seed germination. In: *Seed dispersal and frugivory: ecology, evolution and conservation* (Ed.

by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 339-350. New York: CAB International.

Valenta, K. & Fedigan, L. M. 2009. Effects of gut passage, feces, and seed handling on latency and rate of germination in seeds consumed by capuchins (*Cebus capucinus*). *American Journal of Physical Anthropology*, 138, 486-492.

Verdú, M. & Traveset, A. 2005. Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. *Ecology*, 86, 1385-1394.

Wehncke, E. V. & Dalling, J. W. 2005. Post-dispersal seed removal and germination selected tree species dispersed by *Cebus capucinus* on Barro Colorado Island, Panama. *Biotropica*, 37, 73-80.

Whitington, C. L. 1992. Interactions between lar gibbons and pig-tailed macaques at fruit sources. *American Journal of Primatology*, 26, 61-64.

Wrangham, R. W., Chapman, C. A. & Chapman, L. J. 1994. Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology*, 10, 355-368.

In the previous chapter we showed that northern pigtailed macaques are effective seed dispersers for many plant species as they disperse many seeds of many fruit species, of all kind of size, in all forest types, from primary forest to secondary forest, thanks to various handling techniques, and with a neutral effect on the seed germination and viability of most plant species.

~~~

Seed dispersal distance is an important component of dispersal quality. Thus the way animal move may have an impact on their seed dispersal effectiveness. In the next chapter, we will investigate the travels made by a troop of northern pigtailed macaques and then discuss the consequences in term of seed dispersal.
~~~

CHAPTER 3

Influence of wild and human food resources on ranging patterns of northern pigtailed macaques (*Macaca leonina*)

Albert, A., Savini, T., Huynen, M.-C. Influence of wild and human food resources on ranging patterns of northern pigtailed macaques (*Macaca leonina*). Submitted to the American Journal of Primatology.

Résumé

De nombreuses études ont mis en évidence l’influence de la disponibilité en nourriture sur la taille et la localisation du domaine vital des primates. Notre étude vise à déterminer comment la disponibilité en fruits influe sur les déplacements d’une troupe de macaques à queue de cochon du Nord (*Macaca leonina*) vivant autour du centre des visiteurs du parc national de Khao Yai, Thaïlande. Nous prédisions que les macaques devraient augmenter leurs déplacements lors des périodes de faible abondance de fruits pour atteindre une quantité suffisante de nourriture de haute qualité, et qu’ils devraient aller là où il y a le plus de fruits ou là où il y a le plus de fruits de certaines espèces en particulier. De plus, la présence des humains devrait aussi influencer la localisation de leur domaine vital. Nous avons suivi une troupe pendant 12 mois et enregistré son régime alimentaire et ses mouvements dans le domaine vital (points GPS toutes les 30 minutes). Pour faciliter les comparaisons spatiales entre les trajets des macaques et la disponibilité en fruits, nous avons apposé une grille, comprenant des cellules de 110 x 110 m, sur les kernels mensuels définissant la surface du domaine vital. La distribution spatio-temporelle des arbres en fruits sur des transects botaniques a été analysée puis convertie en un indice d’abondance de fruits. Nos résultats ont montré qu’en mars les macaques augmentaient la taille de leur domaine vital, probablement pour obtenir une quantité suffisante de fruits nouvellement disponibles. D’avril à août, suivant nos prédictions, ils se sont déplacés en direction de certaines espèces de fruits. En septembre, les fruits sont redevenus rares et les macaques ont augmenté la taille de leur domaine vital, probablement pour trouver assez de fruits avant une totale pénurie. D’octobre à février, contrairement à nos prédictions, ils ont diminué la taille de leur domaine vital et ont inclus de a nourriture humaine, un item de haute qualité, dans leur régime alimentaire. En conclusion, les macaques utilisaient plusieurs stratégies de déplacement, en fonction des disponibilités en fruits et en nourriture humaine.

Mots-clés **:** taille de domaine vital ; disponibilité des ressources ; parc national de Khao Yai ; Asie du sud-est.

Abstract

Numerous studies have highlighted the influence of food availability on primates' home range size and location. Our research aims to determine how fruit availability impacts the ranging patterns of a troop of northern pigtailed macaques (*Macaca leonina*) living around the Visitor Center of the Khao Yai National Park, Thailand. We predicted that macaques should increase their range during low fruit abundance periods to gather sufficient high-quality food, and that they should go where there is more fruits or more fruits of some particular species. Moreover, the presence of humans should also influence their home range location. We followed a troop over a period of 12 months and recorded its diet and movements within the home range (GPS points every 30 minutes). On monthly kernels defining the monthly home range surface, we superimposed a grid of 110 x 110 m cells to facilitate spatial comparisons between macaques' travel and food availability. We analyzed the spatio-temporal distribution of fruiting trees in botanical transects and converted it into a fruit productivity index. Our results showed that in March, they increased their home range probably to obtain a sufficient amount of newly available fruits. From April to August, following our prediction, they traveled toward some particular fruit species. In September, fruits became more rare again and macaques increased their home range perhaps to find enough fruits as supplies began to dwindle. From October to February, contrary to our predictions, they decreased their home range size and included human food, a high-quality item, in their diet. In conclusion, the macaques used several ranging strategies according to fruit and human food availability.

Key words**:** home range size; resource availability; Khao Yai National Park; Southeast Asia.

Introduction

One of the most obvious adaptations of animals to their environment relates to the variation of their home range location and size according to the environment which typically undergoes temporal variations (*i.e.* baboons (Bronikowski & Altmann 1996), macaques (Hanya et al. 2006), woolly monkeys (Di Fiore 2003), gorillas (Vedder 1984), golden monkeys (Twinomugisha & Chapman 2007), capuchin monkeys (Robinson 1986), and tamarins (Culot et al. 2010)). The characteristics of a species' home range are defined by the requirements of a species in terms of survival and reproduction. Thus the daily path length and the size of a home range may be influenced by body size (Milton & May 1976), group size (Clutton-Brock & Harvey 1977; Dunbar 1988; Fashing et al. 2007; Izumiyama et al. 2003; Makwana 1978; Olupot et al. 1994), reproductive efforts, sex, age, interactions among conspecific groups (Isbell 1983), habitat structure (Izumiyama et al. 2003), and weather conditions (Clutton-Brock & Harvey 1977; Isbell 1983), but also diet (Boonratana 2000; Clutton-Brock & Harvey 1977; Harvey & Clutton-Brock 1981; Milton & May 1976), foraging strategies, and, finally, the availability of food resources, known to be a major determinant of home range variations in many animal species (Bourgoin 2008; Brito 2003; Ferguson et al. 1999; McLoughlin & Ferguson 2000; Whitaker et al. 2007; Zabel et al. 1995), including primates (Di Fiore 2003; Hanya et al. 2006; Harvey & Clutton-Brock 1981; Isbell 1983; Kaplin 2001; Olupot et al. 1997; Porter et al. 2007; Robbins & McNeilage 2003; Twinomugisha & Chapman 2007).

Seasonality of fruit production in tropical forests, along with the heterogeneous distribution of fruiting trees over the home range, induce spatio-temporal variations in the distribution of resources of frugivorous primates (Ricklefs 1990). It is thus necessary for most animals to find a trade-off between their needs and the cost to meet them. They should optimize their ranging distance to minimize the costs, *i.e.* energy cost of travel as well as risk of predation or competition, and maximize the benefits, *i.e.* food rewards (Barrett 2009; Ricklefs 1990; Zhao 1999).

Studies have highlighted two possible patterns used by animals to respond to the seasonal decreases in food availability. For some species, the periods with high food availability allow a decrease in the ranging distances, whereas the scarcity of fruits forces them to range farther to obtain a sufficient amount of their original diet (energy-maximizing strategy; *e.g.* Milton 1980; Vedder 1984). For other species, when the availability of food is high, the energy gain allows ranging farther to reach preferred food species. In contrast, food scarcity may force them to decrease their ranging distance to compensate for low energy availability resulting from the consumption of lesser-quality items (energy-minimizing strategy; *e.g.* Agostini et al. 2010; Di Fiore 2003; Hanya et al. 2006; Swedell 2002). Some authors have shown that both strategies could be used by a single species according to the availability of some particular fruit species or other items (Agetsuma and Noma 1995). Our aim is to determine the ranging and feeding strategy, energy-maximizing and/or minimizing, used by a primate troop according to food availability.

During our study of the feeding ecology of a habituated troop (HQ troop) of northern pigtailed macaques (*Macaca leonina*) at Khao Yai National Park, Thailand, we systematically collected data on ranging behavior. Northern pigtailed macaques are semi-terrestrial and mainly move on the ground, which decreases the costs of long daily paths (Rodman 1979). They are frugivorous as are many other cercopithecine species. The home range size of the closely related southern pigtailed macaque, *Macaca nemestrina*, has been estimated to be between 62 and 828 hectares (Sponsel et al. 2002). The ranging pattern of northern pigtailed macaques seems to fit the definition of a multiple central place foraging strategy (Chapman et al. 1989). Indeed, northern pigtailed macaques use daily round-trips between a limited number of central places (sleeping sites) and feeding sites (Albert et al. 2011).

In most primates, proximity to human settlements means abundance of human food (Altmann & Muruthi 1988; Brotcorne et al. 2011; Ram et al. 2003). Our study troop lived around the park Visitor Center and was often observed either stealing food from houses or trash cans, or begging from tourists. Feeding on human food may have consequences on their ranging behavior, as demonstrated in other primate species (Saj et al. 1999; Strum 2010).

In this study, we examined whether the ranging behavior of this troop of pigtailed macaques was associated with the seasonal resource availability, fruits as well as human food. We predicted that the troop's ranging pattern should be affected by seasonal variation in fruit availability as they are mainly frugivorous and that, in low food abundance periods, they should increase their foraging area (*i.e.* energy-maximizing strategy) instead of adjusting their diet, as do more arboreal species such as *Macaca fascicularis* (Lucas & Corlett 1991). Moreover, they should spend more time were there is more fruits in total or, alternatively, were there is more fruits of some particular species. Finally, the location of their home range should be affected by the location of human food.

Methods

Study area

This study was conducted at Khao Yai National Park (KYNP; 2,168 km²; 14° 05'–15'N, 101° 05'–50'E). The study site is located around the park Visitor Center, an area of seasonally wet evergreen forest (Forest Restoration Research Unit 2000) at 700-800 m ASL and including a ranger station and various tourist facilities. The climate is monsoonal, with a wet season (from May to October) and a relatively dry season divided into a cool (from November to February) and a hot (from March to April) period. The mean monthly temperature ranges from 19°C (December, January) to 24°C (March, April) and the annual precipitation averages 2,504 mm with monthly averages of 69 mm in the dry season and 353 mm in the wet season (2006-2009). Rainfall and temperature patterns were similar over the study years (Conservation Ecology Program, KMUTT, pers. com.).

Data collection

The study troop (HQ troop) included 32 to 39 individuals: 2 to 3 adult males and 12 to 13 adult females (full grown and sexually mature) individually identified, along with 1 to 3 sub-adult males and 17 to 20 juveniles. A.A. was the only observer and conducted all data collection. She followed the study troop for one day every two or three days, from sleeping site to sleeping site, *i.e.* approximately from 6:00am to 6:00pm. The follow averaged 7.25 days per month, spreading over a average of 19 days per month, and totalizing 1,029 hours. We divided the study in three periods for logistical reasons (April - July 2009 [Period 1]: 370 h; December 2009 - March 2010 [Period 2]: 288 h; August - November 2010 [Period 3]: 371 h). Common distances between macaques and the observer were between 1 and 10 m.

During each period, the observer noted the troop's locations based on GPS coordinates automatically recorded every 30 minutes to maximize independence between two consecutive points (Phoonjampa et al. 2010). The GPS records averaged 182 GPS positions per month which appeared to be a representative sample of the total locations per month visited by the macaques (Downs 2008; Seaman et al. 1999). To ensure that we collected enough data to create monthly home ranges, we checked if the accumulation curve of monthly home range size reached an asymptote. The GPS locational errors ranged from 6 to 10 m. To determine the degree of home range use, we defined a "presence index" as the number of observations recorded in the various parts of the home range. We then used the software ArcView 3.2a (ESRI) to map the monthly home range, simultaneously reporting the values (in percentages) of the presence index in specified locations, and the length of daily travel. We derived estimates of limits and surface of the day range using the least square cross-validated fixed kernel density estimation (LSCV KDE, hereafter referred to as kernel), one of the most widely used and the most accurate estimation method for home range size (Seaman & Powell 1996; Worton 1989). We defined the monthly home ranges by the 95% kernels and removed the outlying points, *i.e.* 5% of the sample location points, from the analysis to avoid any bias due to exploratory and/or exceptional movements (Getz et al. 2007). The core areas were defined by the 50% kernels.

Within the troop home range, we distinguished two types of habitat (Figure 3.1): human settlements and forests. The "*human settlements*" habitat included tourist and associated buildings (staff housing, restaurants, bungalows), as well as the road crossing the tourist area, other housing, a section of the river and a small section of forest directly adjacent. The "*forests*" habitat refers to the continuous natural forest and the river crossing the study area that were > 10 m away from the human settlements.

In addition, we distinguished five sub-types of forest, according to successional stages. The "*grassland*" is essentially composed of Gramineae. The "*shrubland*" is composed of shrubs, predominantly *Melastoma malabathricum*, and grass. The "*small tree*" areas are dominated by treelets with a DHB between 10 and 20 cm (> 80% of trees) and below 15 m high, *i.e.* mainly *Eurya nitida*, *Cratoxylum cochinchinense* and *Schima wallichii*, and some shrubs. The "*secondary forest*" is mainly composed of trees with a DBH between 10 and 20 cm (> 70% of trees) but predominantly taller than 15 m, and has lower species diversity than primary forest (essentially *Cratoxylum cochinchinense*, *Eurya nitida*, *Machilus odoratissima*, *Schima wallichii*, and *Symplocos cochinchinensis* trees). The "*primary forest*" is characterized by trees of all age and size classes, lianas, epiphytes and hemi-epiphytes, and high species diversity. We noted the time at every change in habitat and forest type during the macaques' movements to calculate their proportion of use.

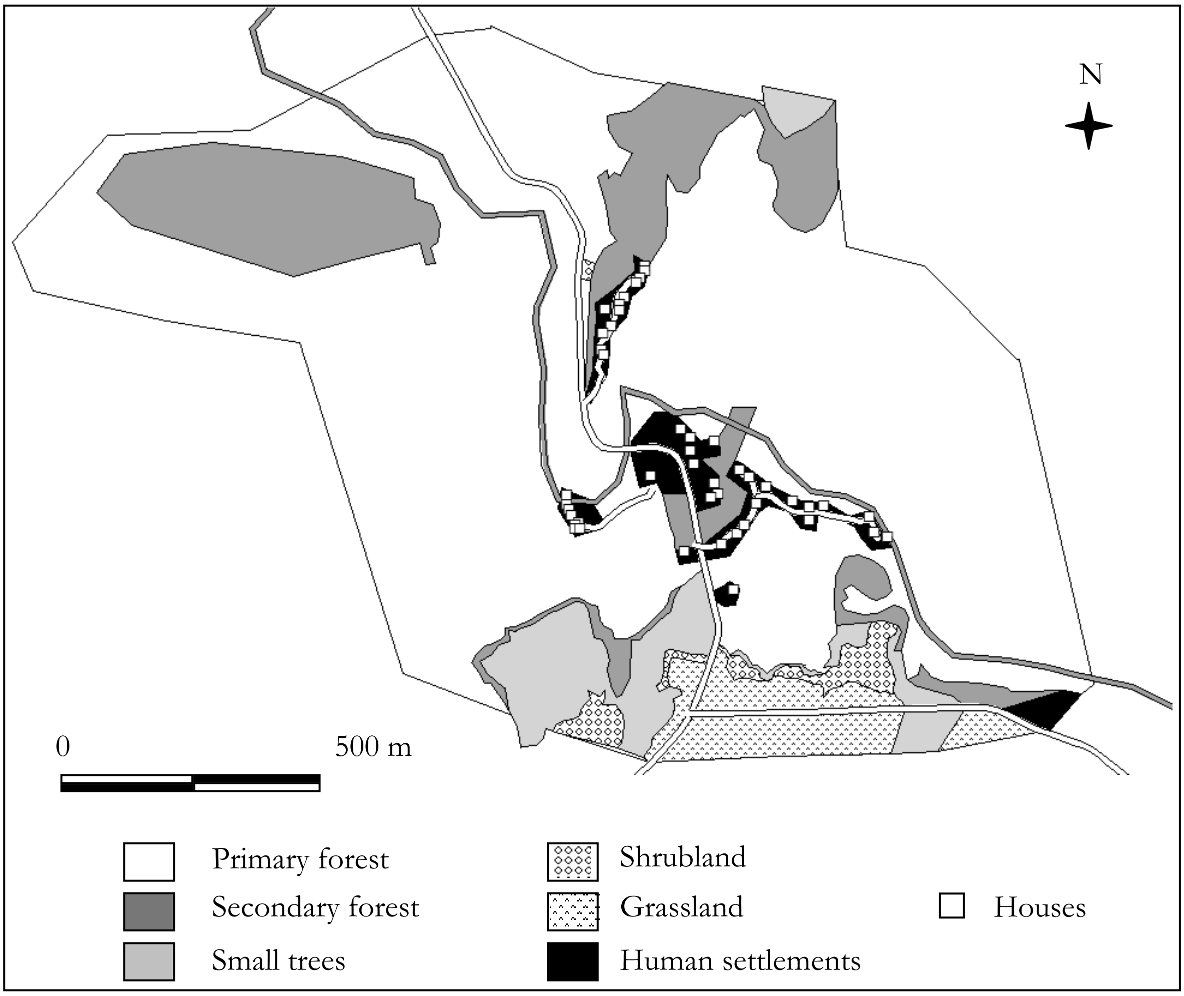


Figure 3.1. Spatial representation of the various habitat types in the studied troop's home range.

The observer created 12 botanical transects oriented north–south across the troop's home range to evaluate the spatial distribution and density of resources. Transects were twenty meters wide and about 110 meters spaced to cover a total area of 27 ha, *i.e.* approximately 20% of the home range (Mueller-Dombois & Ellenberg 1974; Savini et al. 2008; Struhsaker 1975). The observer measured, tagged, mapped and identified all trees with a DBH ≥ 10 cm. In the nearby Mo Singto Long Term Biodiversity Research Plot (Brockelman 1998), with a plant composition identical to that found in the home range, we evaluated the overall availability of fruit species by recording monthly the phenology of about ten individuals of each plant species included in the home range. We defined a 5-point scale score to quantify fruits in the crown of a tree, with 0 = no fruit, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, and 4 ≥ 76%**.**

The observer used scan sampling (Altmann 1974) of all visible members of the troop at intervals of 30 min (N = 21,389 observations) to record, for each individual, the item and plant species consumed in case of feeding events.

The observer collected fresh feces found in the forest. She sieved them through a 0.5 mm nylon mesh to extract the seeds and identified the plant species. Most *Ficus* species seeds, typically indistinguishable, were not identifiable to the species level. We grouped these species into *Ficus* spp. Seed species that could not be identified were assigned an identification number.

We assessed plant species importance in the diet based on fecal and scan samples using the definitions of Doran et al. (2002). We defined important plant species as plants consumed in large quantities (*i.e.* in at least 50% of fecal samples during at least one month) and/or for long duration (*i.e.* in feces for at least 50% of months). In addition, we also considered all plant species consumed during at least 5% scan sampling observations as important species.

Data analysis

In order to compare the troop's ranging behavior with the spatio-temporal distribution of fruits in the home range during a given month, we used a sampling grid of 110x110m cells covering the home range. Each cell included a section of botanical transect (18% of a cell trees were part of the section). For each month m of the study we calculated a fruit abundance index for each tree species k per cell c (SFAI_{kcm}) [Eq. (1)].

$$\mathrm{SFAI}_{kcm} = \mathrm{D}_c\mathrm{B}_{kc}\mathrm{P}_{km} \qquad (1)$$

where D_c is the density of a given species in a given cell c (stems/cell), B_{kc} is the mean basal area of trees of a given species k in the cell c (m^2/cell), and P_{km} is the mean phenology score of fruit in the crown of species k in a given month m. Then, we added the results of every species found in each cell to obtain a monthly fruit abundance index (Savini et al. 2008) per cell (FAI_{cm}) [Eq. (2)].

$$\mathrm{FAI}_{cm} = \sum_{k=1}^{n} \mathrm{SFAI}_{kcm} \qquad (2)$$

Finally, we added the results of every cell in a given month to obtain a monthly total fruit abundance index (TFAI_m) [Eq. (3)].

$$\mathrm{TFAI}_m = \sum_{c=1}^{n} \mathrm{FAI}_{cm} \qquad (3)$$

To classify each month in high or low fruit abundance periods, the monthly TFAI scores were first ranked. To minimize the potential bias resulting from an overlap in confidence intervals of high and low TFAI scores, we divided the TFAI scores' distribution into three classes. High fruit abundance periods were defined as months with TFAI scores above the 66% quantile. Low fruit abundance periods were defined as months with TFAI scores below the 33% quantile. Any case which split the sample in two, using either the median or the mean as the threshold between periods of high and low TFAI, gave similar results.

We performed two-tailed statistical tests with Statistica 9.0 (α level: 0.05). We conducted Mann-Whitney *U*-tests in order to compare the potential difference in monthly home range size, daily path length, diet, and time spent in each forest and habitat type between high and low fruit abundance periods.

To highlight possible relationships between macaques' movements and diet with fruit availability, we performed Spearman rank correlations successively between daily path length, diet, and TFAI, and between TFAI and monthly home range size, and between FAI and the presence of macaques in each cell for each month. To test the alternative hypothesis that they spent more time where there were more fruits of some particular species, we replaced the total FAI by the SFAI (*i.e.* the FAI of each species).

We calculated binomial probabilities of differences between the use frequency of each forest and habitat type (from the number of GPS points made during the follow) and the frequency expected given the area of each type.

The present study was approved by the Department of National Parks, Wildlife, and Plant Conservation, Bangkok, was conducted in full compliance with the laws of the Kingdom of Thailand, and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

Results

Availability of resources

Among the 126 fruit species that were part of the troop's diet, the abundance of 42 was possible to analyze (*i.e.* they were found on botanical transects, with phenology data available). Moreover, 117 sampling cells were analyzed: macaques visited 103 cells and fed in 93 cells. There was a significant positive correlation between the time the troop spent in each cell and the feeding plant density (*i.e.* plants macaques were observed feeding on fruit) (Spearman correlation: $N = 117$; $r_S = 0.87$; $P < 0.001$). Over the course of the study, the mean fruit abundance index in the home range was 8131 per cell and ranged from 1518 in November 2010 to 27,725 in May 2009 (Figure 3.2). The productivity peak began in March, two months before the wet season, and started to decline in August, three months before the dry season. Human food was available year round due to the constant presence of tourists and local people.

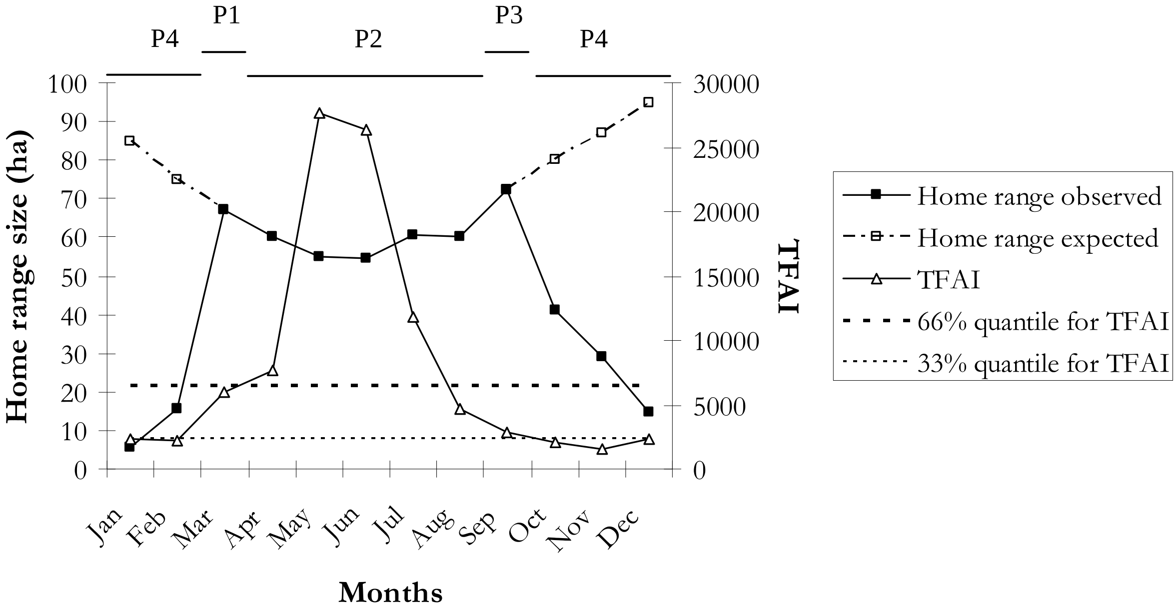


Figure 3.2. Variation of home range size and total fruit abundance index (TFAI) according to months. High fruit abundance periods were defined as months with TFAI scores being above the 66% quantile. Low fruit abundance periods were defined as months with TFAI scores being below the 33% quantile. The variation of home range size observed differs from what was expected. Human food could be the cause. Period 1 (P1): March; Period 2 (P2): April-August; Period 3 (P3): September; Period 4 (P4): October-February.

Apart for four months of the 12 months of the study (Spearman correlation: $N = 117$; June 2009: $r_S = 0.19$; $P < 0.05$; March 2010: $r_S = 0.28$; $P < 0.05$; August 2010: $r_S = 0.19$; $P < 0.05$; September 2010: $r_S = 0.20$; $P < 0.05$) the time the troop spent in a cell was not correlated with the fruit abundance index of all species (FAI). However, by testing our alternative hypothesis, we found that the time macaques spent in a cell was positively correlated with the fruit abundance index of some particular species (SFAI) found in the same cell for each month of the study (except January 2010) (Appendix 3.1).

Diet

Over the study period, 1818 feeding observations were recorded during scan sampling and 335 feces were collected. The HQ troop ate parts from 138 plant species, including 126 fruit (including at least 16 *Ficus* species), seven flower, six pith, six leaf, and four shoot species. They also ate human food (rice, fruits, bread, biscuits, *etc.*), fungi, ants, termites, spiders, grasshoppers, caterpillars, beetles and some small vertebrates (*e.g.* squirrels). Fifteen plant species were considered as important species in the diet (Chapter 2). The macaques' diet varied from highly frugivorous (> 50% of fruits in the diet) during the high fruit abundance periods, to omnivorous during the low fruit abundance periods (Figure 3.3). The proportion of fruits in the diet was significantly greater in the high fruit abundance periods compared to the low fruit abundance periods (Mann-Whitney U-Test: $U = 0$, $N_{high} = 4$, $N_{low} = 4$, $P < 0.05$), from 8% in January to 76% in June ($N = 1{,}818$ feeding observations during scan sampling) and, conversely, the proportion of human food decreased, although it only approached significance, in the high fruit abundance periods compared to the low fruit abundance periods (Mann-Whitney U-Test: $U = 1$ $N_{high} = 4$, $N_{low} = 4$, $P = 0.061$), from a high of 69% in January to a low of 2% in June. Moreover, there was a significant correlation between the number of fruit species in the diet and the number of species fruiting each month (Spearman correlation: $N = 12$; $r_S = 0.80$; $P < 0.01$). Also the monthly TFAI was directly correlated with the monthly percentage of fruit in the diet (Spearman correlation: $N = 12$; $r_S = 0.88$; $P < 0.001$), and inversely correlated with the monthly percentage of flowers (Spearman correlation: $N = 12$; $r_S = -0.68$; $P < 0.05$) and human food (Spearman correlation: $N = 12$; $r_S = -0.78$; $P < 0.01$) in the diet.

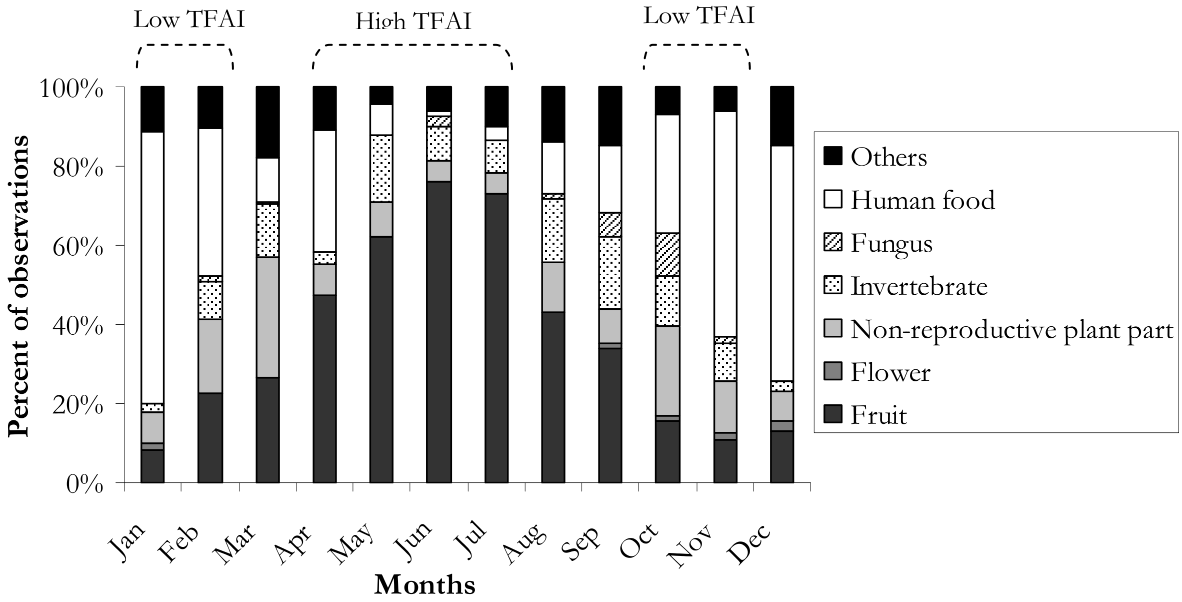


Figure 3.3. Seasonal variation in the diet of the studied troop. TFAI = total fruit abundance index. N_{Jan}=123 feeding observations during scan sampling; N_{Feb}=132; N_{Mar}=170; N_{Apr}=113; N_{May}=203; N_{Jun}=142; N_{Jul}=126; N_{Aug}=211; N_{Sept}=197; N_{Oct}=133; N_{Nov}=171; N_{Dec}=97.

Daily path length, area use and behavioral activities

Neither the monthly home range size (Spearman correlation: $N = 12$; $r_S = 0.54$; $P > 0.05$) nor the mean daily path length (Spearman correlation: $N = 12$; $r_S = 0.52$; $P > 0.05$) was correlated with the TFAI. However, over the study period, the mean daily path length of the troop was 1588 ± 412 m ($N = 86$ complete days) and increased significantly during the high fruit abundance periods ($\mathrm{mean}_{\mathrm{high}} = 1804 \pm 471$ m; $\mathrm{mean}_{\mathrm{low}} = 1567 \pm 325$ m; Mann-Whitney U-Test: $U = 258$, $N_{high} = 30$, $N_{low} = 27$, $P < 0.05$). Moreover, the size of the monthly home range varied from 5.8 ha (January 2010) to 72.4 ha (September 2010) with two peaks (67.3 ha in March 2010 and 72.4 ha in September 2010) (Figure 3.4), and was significantly larger during the high (mean = 57.8 ± 3.3 ha) than during the low (mean = 38.3 ± 25.9 ha) fruit abundance periods (Mann-Whitney U-Test: $U = 0$, $N_{high} = 4$, $N_{low} = 4$, $P < 0.05$). The size of the core area (50% kernel) varied from 0.5 ha (January 2010) to 11.0 ha (September 2010). The location of the home range varied from month to month (Figure 3.4). These monthly variations did not seem to be due to an insufficient number of study days as, for 10 of 12 months, the accumulation curve of the home range size reached an asymptote.

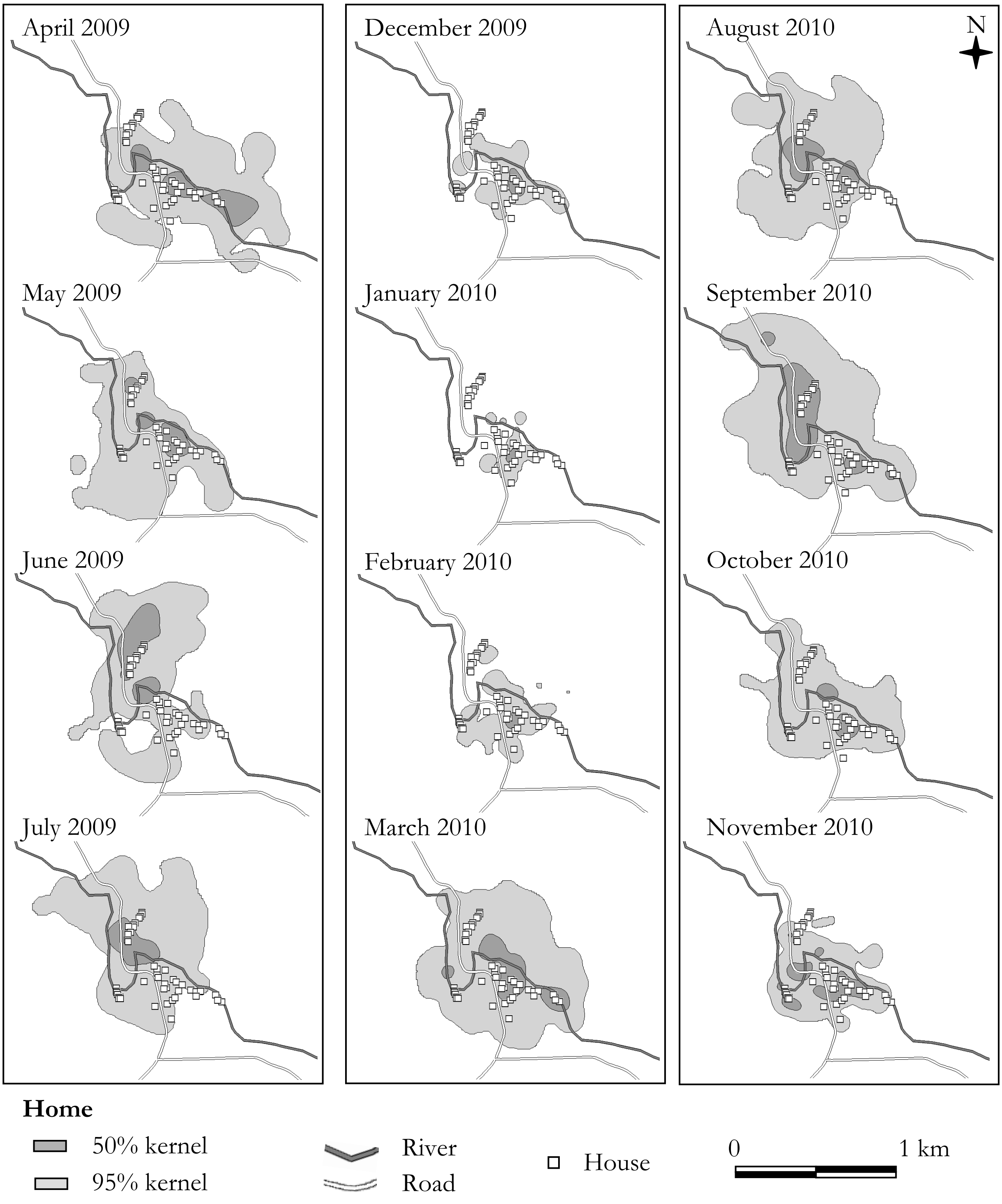


Figure 3.4. Seasonal variation in size and location of monthly home ranges (50% and 95% kernels). High fruit abundance period: April, May, June, July. Low fruit abundance period: January, February, October, November.

The mean daily path length was positively correlated with the monthly percentage of fruits in the diet (Spearman correlation: $N = 12$; $r_S = 0.67$; $P < 0.01$) and negatively correlated with the monthly percentage of human food consumed (Spearman correlation: $N = 12$; $r_S = -0.68$; $P < 0.01$). The more macaques ate fruits (and the less they ate human food), the longer distance they traveled.

Use of habitat and forest types

The home range was mainly covered by primary forest (Figure 3.1). The troop spent 46% of the study time ($N = 1029$ hours) in the forests and 54% in human settlements. When in the forests, it spent 69% of the study time in primary forests, 30% in secondary forests, and less than 1% in small tree areas, shrublands and grasslands. The use of forest was more intensive during the high fruit abundance periods (mean = 60 ± 11%) than during the low fruit abundance periods (mean = 36 ± 17%), contrary to the use of human settlements ($\text{mean}_{\text{high}} = 40 \pm 11\%$; $\text{mean}_{\text{low}} = 64 \pm 17\%$; Mann-Whitney *U*-Test: $U = 0$, $N_{high} = 4$, $N_{low} = 4$, $P < 0.05$).

The troop used much more frequently the human settlements area and the secondary forest than expected (Binomial probability: $P = 0$), and used less frequently the various other types of forest ($P < 0.001$).

Discussion

This study indicated that the macaque troop adjusted its diet and ranging behavior according to seasonal variations of wild resources. The positive relationships between the quantity of fruits in the diet and the quantity of fruits available in the home range show that the more there were fruits, the more macaques ate fruits. This relationship was also supported by the increased use of forest habitats by the macaques during the high fruit abundance periods. Then, the monthly home range size and daily path length of the troop decreased during the low fruit abundance periods. This pattern is contrary to our prediction as it corresponds to the energy-minimizing strategy, also found in other primate species (Agostini et al. 2010; Di Fiore 2003; Hanya et al. 2006; Swedell 2002). During low fruit abundance periods, the macaques spent more time near human settlements where they used human food, which is frequent in Cercopithecinae living close to humans. However, contrary to our studied troop, cercopithecines usually eat it in quantity year round (Naughton-Treves et al. 1998; Brotcorne pers. com.). The lack of correlations between the FAI and the macaques' presence in each cell suggests that macaques did not spend more time where there were more fruits. However, the correlation between the SFAI of some particular plant species and the time macaques spent in a cell (Appendix 3.1) show that their travels were directed toward places containing particular fruit species, some of which were qualified as important in the troop‘s diet. This specific ranging behavior has also been shown in other primates (Kaplin 2001; Milton 2000). However, our analysis did not included lianas, palm trees and small trees (DBH<10cm), which were an important part of the diet during some months of the study and thus could have also influenced the travel direction of the macaques (*e.g. Diplectria barbata* (liana) in June and July; *Toddalia asiatica* (liana) in July; *Daemonorops jenkinsiana* (Palm tree) in October, November and January; *Melastoma malabathricum* (shrub) in May).

These results would initially seem to contradict our prediction that macaques would enlarge their exploited area in times of fruit scarcity (*i.e.* energy-maximizing strategy). Instead, they minimized their travel costs by decreasing their daily path length and home range size, and changed their diet by including human food. This diet flexibility is rather common in primates (Chapman 1987, 1988; Chapman & Chapman 1990; Clutton-Brock & Harvey 1977; Lindburg 1977; Milton 1980). However, the detailed study of the macaques' ranging pattern and diet suggests they used both strategies. First, the variation in monthly home range size was not simply unimodal but bimodal and could be divided into four periods: (1) a peak in March when rainfall began, (2) a slight decrease with a plateau during the high fruit abundance periods, (3) a new peak in September, and (4) a decrease in size during roughly the dry season (from October to February) (Figure 3.2).

During period 1, in March, macaques seemed to use an energy-maximizing strategy by increasing their home range size to procure a sufficient amount of fruits. This period corresponds to the beginning of rainfall, when fruits started to be available but were still relatively scarce. One could also hypothesize that the troop did not only increase its range to eat but also to monitor the phenological state of trees in a larger area and increase its probability to find fruits later.

During period 2, macaques traveled toward preferred fruiting species and consumed them until their fruits began to become scarce and/or until another preferred species fruited. Their preference for sites with a lower fruit abundance (FAI) and higher abundance of particular fruit species (SFAI) instead of sites with higher fruit abundance (FAI) suggests that northern pigtailed macaques are capable of spatial discounting as already shown in other primate species (*e.g.* Stevens et al. 2005). Moreover, our observations showed that northern pigtailed macaques could be a "traplining" species (Janson 2000). Indeed, the troop usually visited the same patches of fruiting trees in predictable repeating sequences during several days or even weeks (Figure 3.5). Despite the availability of human food year round, macaques feeding mainly on fruit during this period suggests that fruit was either of higher quality than or preferred over human food, maybe because they were harassed by local people and felt unsafe where human food was located (Foerster & Monfort 2010).

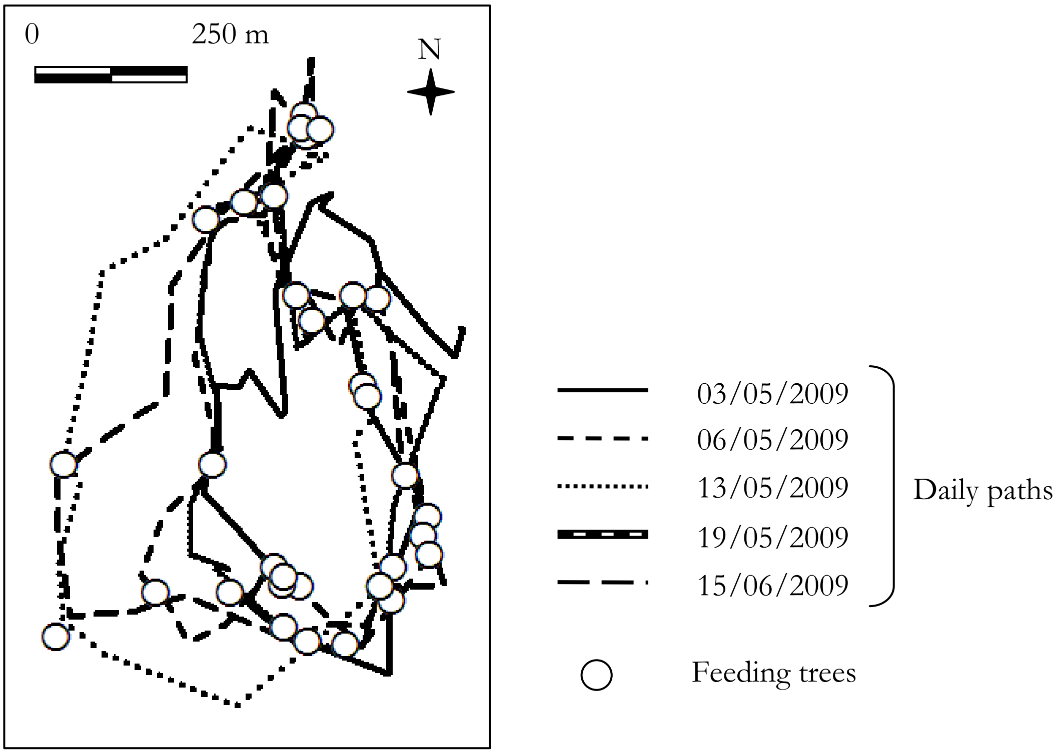


Figure 3.5. Example of five daily paths showing that macaques used the same patches of resources during several days or even weeks.

During period 3, in September, fruits started to be scarce again. Macaques used an energy-maximizing strategy and increased their home range size, probably to reach enough fruits before fruit availability reached its lowest point.

Finally, during period 4, macaques seemed to show an energy-minimizing strategy: they decreased their travel costs by staying nearby human settlements, thus decreasing their home range size. However, they did not include, in their diet, low-quality items, as predicted, but human food, which is considered as a high-quality item, often of high caloric density, palatability, and digestibility (Forthman-Quick 1986; Saj et al. 1999).

Hamilton and Watt (1970) suggested four potential strategies used by animals in the exploitation of energy: (1) minimize the probability of decline of energy balance below zero, (2) maintain energy balance at zero, (3) increase energy balance above zero, and (4) maximize energy with no limits. The study troop seemed to have found a method of maximizing energy with no limits. During the dry season, the high quality of human food and its high concentration at the Visitor Center should give it higher value than any other item available (non-reproductive plant parts and aseasonal fruiting species such as *Ficus* spp. or Palmae trees) given the energy needed to gain access to these other items. The use of human food during the low fruit abundance periods has already been shown in studies of crop-raiding by primates (*e.g.* Naughton-Treves et al. 1998), with a higher use of some crops by primates during periods of wild fruit scarcity.

This particular pattern of ranging leads us to think that, without human food, macaques would tend to use, as predicted, an energy-maximizing strategy (Figure 3.4). This behavior as been shown in a troop of *Chorocebus aethiops* (Barrett 2005), another semi-terrestrial cercopithecine species that tended to increase its home range size during fruit scarcity. The study of other troops, living in more remote areas, would help to confirm our hypothesis.

Acknowledgments

We thank the Department of National Parks, Wildlife and Plant Conservation and the National Research Council of Thailand for granting research permission, and the superintendent of Khao Yai National Park for his hospitality. We thank George Gale and Lee Olsen for editing the English and Alain Hambuckers for helping in statistical analysis. We are grateful to Andreas Koenig for his helpful comments on the manuscript. This study was carried out with the financial support of the University of Liège, Belgium (A.A), and that of the Biodiversity Research and Training Program, Thailand (Grant No. BRT R_349007) (T.S. and M-C.H.). The research was approved by the Department of National Parks, Wildlife, and Plant Conservation, Bangkok, conducted in full compliance with the laws of the Kingdom of Thailand, and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

Appendix

Appendix 3.1. Spearman correlations between the time macaques spent in each cell and the SFAI of species found in these cells for each month of the study. *N* = number of cells analyzed = 117. NS = non significant ($P > 0.05$).

	Adinandra integerrima	*Aglaia elaeagnoidea*	*Albizia attopeuensis*	*Alchornea rugosa*	*Alphonsea boniana*	*Anthocephalus chinensis*	*Antiaris toxicaria*	*Ardisia nervosa*	*Ardisia sanguinolenta*	*Baccaurea ramiflora*
Apr 2009		$r_s = -0.18$ NS			$r_s = -0.17$ NS					$r_s = -0.03$ NS
May 2009			$r_s = -0.01$ NS		$r_s = 0.03$ NS					$r_s = 0.27$ $P < 0.01$
Jun 2009			$r_s = 0.20$ $P < 0.05$		$r_s = 0.00$ NS					
Jul 2009			$r_s = 0.00$ NS		$r_s = 0.05$ NS	$r_s = 0.06$ NS				
Dec 2009									$r_s = -0.02$ NS	
Jan 20010										
Feb 2010									$r_s = 0.17$ NS	$r_s = 0.02$ NS
Mar 2010					$r_s = 0.02$ NS				$r_s = 0.16$ NS	$r_s = 0.26$ $P < 0.01$
Aug 2010					$r_s = 0.21$ $P < 0.05$	$r_s = 0.14$ NS		$r_s = 0.07$ NS	$r_s = 0.03$ NS	
Sept 2010		$r_s = -0.08$ NS				$r_s = 0.30$ $P < 0.01$		$r_s = -0.13$ NS		
Oct 2010		$r_s = -0.09$ NS				$r_s = 0.13$ NS		$r_s = -0.07$ NS		
Nov 2010		$r_s = -0.16$ NS				$r_s = 0.10$ NS		$r_s = -0.15$ NS		

	Balakata baccata	*Bhesa robusta*	*Bridelia insulana*	*Carallia brachiata*	*Celtis tetrandra*	*Choerospondias axillaris*	*Cinnamomum iners*	*Cinnamomum subavenium*	*Decaspermum fructicosum*	*Diospyros glandulosa*
Apr 2009	$r_s = -0.09$ NS		$r_s = -0.22$ $P < 0.05$	$r_s = -0.07$ NS	$r_s = -0.00$ NS	$r_s = -0.06$ NS				$r_s = -0.07$ NS
May 2009	$r_s = 0.03$ NS		$r_s = 0.05$ NS		$r_s = 0.14$ NS	$r_s = 0.29$ $P < 0.01$				$r_s = 0.14$ NS
Jun 2009	$r_s = -0.05$ NS				$r_s = 0.20$ $P < 0.05$	$r_s = 0.17$ NS				$r_s = 0.24$ $P < 0.05$
Jul 2009					$r_s = 0.45$ $P < 0.001$	$r_s = 0.30$ $P < 0.01$				$r_s = 0.22$ $P < 0.05$
Dec 2009					$r_s = 0.05$ NS			$r_s = 0.01$ NS		
Jan 20010					$r_s = 0.02$ NS			$r_s = -0.10$ NS		
Feb 2010			$r_s = -0.04$ NS	$r_s = -0.11$ NS	$r_s = -0.04$ NS			$r_s = 0.00$ NS		
Mar 2010	$r_s = 0.12$ NS		$r_s = 0.05$ NS	$r_s = -0.07$ NS	$r_s = 0.18$ $P < 0.05$	$r_s = 0.18$ $P < 0.05$		$r_s = 0.01$ NS		
Aug 2010						$r_s = 0.18$ NS				$r_s = 0.11$ NS
Sept 2010						$r_s = 0.26$ $P < 0.01$				$r_s = 0.21$ $P < 0.05$
Oct 2010						$r_s = 0.15$ NS				
Nov 2010										

	Elaeocarpus robustus	*Eurya nitida*	*Garcinia benthamii*	*Gironniera nervosa*	*Glochidion rubrum*	*Helicia formosana*	*Knema elegans*	*Lithocarpus thomsonii*	*Litsea monopetala*	*Macaranga denticulata*	*Macaranga gigantea*
Apr 2009			r_s = -0.03 NS	r_s = 0.09 NS		r_s = 0.07 NS	r_s = -0.16 NS	r_s = 0.18 NS			r_s = 0.04 NS
May 2009	r_s = -0.02 NS		r_s = 0.06 NS	r_s = -0.06 NS		r_s = -0.35 $P < 0.001$		r_s = -0.17 NS			
Jun 2009	r_s = 0.13 NS		r_s = 0.00 NS	r_s = -0.13 NS				r_s = -0.13 NS		r_s = 0.12 NS	r_s = 0.19 $P < 0.05$
Jul 2009	r_s = 0.09 NS	r_s = 0.13 NS	r_s = -0.17 NS	r_s = -0.09 NS				r_s = -0.04 NS			r_s = 0.37 $P < 0.001$
Dec 2009				r_s = 0.03 NS		r_s = -0.25 $P < 0.01$	r_s = -0.11 NS	r_s = 0.03 NS			
Jan 20010				r_s = -0.05 NS		r_s = -0.12 NS	r_s = -0.09 NS	r_s = 0.04 NS			
Feb 2010				r_s = 0.11 NS		r_s = -0.05 NS	r_s = -0.05 NS	r_s = 0.14 NS			r_s = 0.07 NS
Mar 2010		r_s = 0.15 NS		r_s = 0.13 NS		r_s = -0.10 NS	r_s = -0.01 NS	r_s = 0.18 NS			r_s = 0.08 NS
Aug 2010	r_s = 0.16 NS		r_s = 0.05 NS	r_s = -0.05 NS		r_s = -0.30 $P < 0.01$					r_s = 0.25 $P < 0.01$
Sept 2010	r_s = -0.01 NS		r_s = -0.13 NS	r_s = -0.01 NS		r_s = -0.28 $P < 0.01$					r_s = 0.27 $P < 0.01$
Oct 2010	r_s = 0.02 NS			r_s = 0.07 NS		r_s = -0.22 $P < 0.05$					
Nov 2010	r_s = -0.06 NS			r_s = 0.10 NS		r_s = -0.23 $P < 0.05$	r_s = -0.09 NS				

	Machilus odoratissima	*Mastixia pentandra*	*Michelia baillonii*	*Nauclea orientalis*	*Nephelium melliferum*	*Platymitra macrocarpa*	*Pouteria stellibacca*	*Saurauia roxburghii*	*Symplocos sumuntia*	*Syzygium siamensis*	*Syzygium syzygioides*
Apr 2009	$r_s = 0.02$ NS		$r_s = 0.23$ $P < 0.05$		$r_s = 0.04$ NS	$r_s = -0.14$ NS					$r_s = 0.13$ NS
May 2009	$r_s = 0.21$ $P < 0.05$	$r_s = -0.16$ NS	$r_s = 0.14$ NS	$r_s = -0.20$ $P < 0.05$		$r_s = -0.10$ NS					
Jun 2009	$r_s = 0.21$ $P < 0.05$	$r_s = -0.06$ NS	$r_s = 0.13$ NS	$r_s = -0.12$ NS		$r_s = 0.02$ NS					
Jul 2009	$r_s = 0.11$ NS	$r_s = -0.19$ $P < 0.05$	$r_s = 0.19$ $P < 0.05$	$r_s = -0.20$ $P < 0.05$		$r_s = 0.01$ NS					
Dec 2009			$r_s = 0.27$ $P < 0.01$			$r_s = -0.08$ NS					
Jan 20010			$r_s = 0.12$ NS			$r_s = -0.11$ NS					
Feb 2010			$r_s = 0.29$ $P < 0.01$		$r_s = -0.11$ NS	$r_s = -0.17$ NS				$r_s = -0.07$ NS	
Mar 2010			$r_s = 0.33$ $P < 0.001$		$r_s = -0.15$ NS	$r_s = -0.08$ NS				$r_s = 0.03$ NS	
Aug 2010		$r_s = -0.10$ NS		$r_s = -0.06$ NS		$r_s = 0.11$ NS					
Sept 2010			$r_s = 0.07$ NS	$r_s = -0.17$ NS		$r_s = -0.05$ NS					
Oct 2010			$r_s = 0.29$ $P < 0.01$			$r_s = -0.09$ NS					
Nov 2010			$r_s = 0.32$ $P < 0.01$			$r_s = -0.10$ NS					

Literature cited

Agetsuma, N. & Noma, N. 1995. Rapid shifting of foraging pattern by Yakushima macaques (*Macaca fuscata yakui*) response to heavy fruiting of *Myrica rubra*. *International Journal of Primatology*, 16, 247-260.

Agostini, I., Holzmann, I. & Bitetti, M. S. D. 2010. Ranging patterns of two syntopic howler monkey species (*Alouatta guariba* and *A. caraya*) in northeastern Argentina. *International Journal of Primatology*, 31, 363-381.

Albert, A., Savini, T. & Huynen, M. C. 2011. Sleeping site selection and presleep behavior in wild pigtailed macaques. *American Journal of Primatology,* 73, 1222-1230.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour,* 49, 227-267.

Altmann, J. & Muruthi, P. 1988. Differences in daily life between semiprovisioned and wild-feeding baboons. *American Journal of Primatology*, 15, 213-221.

Asensio, N., Brockelman, W. Y., Malaivijitnond, S. & Reichard, U. H. 2011. Gibbon travel paths are goal oriented. *Animal Cognition*, 14, 395-405.

Barrett, A. S. 2005. Foraging ecology of the vervet monkey (*Chlorocebus aethiops*) in mixed lowveld bushveld and sour lowveld bushveld of the Blydeberg Conservancy, Northern Province, South Africa. Magister thesis, University of South Africa.

Barrett, A. S. 2009. Spatial and temporal patterns in resource dispersion and the structure of range use and co-existence in a social omnivore *Chlorocebus aethiops*. PhD thesis, University of South Africa.

Boonratana, R. 2000. Ranging behavior of proboscis monkeys (*Nasalis larvatus*) in the Lower Kinabatangan, Northern Borneo. International Journal of Primatology, 21, 497-518.

Bourgoin, G. 2008. Etude des variations spatio-temporelles de l'activité et de l'utilisation des ressources par les herbivores. PhD thesis, Université Claude Bernard.

Brito, J. C. 2003. Seasonal variation in movements, home range and habitat use by male *Vipera latastei* in Northern Portugal. *Journal of herpetology*, 37, 155-160.

Brockelman, W. Y. 1998. Long term ecological research plot for the study of animals diets in Khao Yai National Park. In: *The Asian Hornbills: Ecology and Conservation*. Thai Studies in Biodiversity 2 (Ed. by Poonsawad, P.), pp. 307-310. Bangkok: Biodiversity Research and Training Program, National Center for Genetic Engineering and

Biotechnology with support from the Thailand Research Fund in collaboration with Science Society of Thailand.

Bronikowski, A. M. & Altmann, J. 1996. Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behavioral Ecology and Sociobiology*, 39, 11-25.

Brotcorne, F., Wandia, I. N., Rompis, A. L. T., Soma, I. G., Suartha, I. N. & Huynen, M. C. 2011. Recent demographic and behavioural data of *Macaca fascicularis* at Padangtegal, Bali (Indonesia). In: *Monkeys on the edge: ecology and management of long-tailed macaques and their interface with humans* (Ed. by Gumert, M. D., Fuentes, A. & Jones-Engel, L.), pp. 180-183. Cambridge Cambridge University Press.

Chapman, C. 1987. Flexibility in diets of three species of Costa Rican primates. *Folia primatologica*, 49, 90-105.

Chapman, C. 1988. Patterns of foraging and range use by three species of neotropical primates. *Primates*, 29, 177-194.

Chapman, C. A. & Chapman, L. J. 1990. Dietary variability in primate populations. *Primates*, 31, 121-128.

Chapman, C. A., Chapman, L. J. & McLaughlin, R. L. 1989. Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. *Oecologia*, 79, 506-511.

Clutton-Brock, T. H. & Harvey, P. H. 1977. Species differences in feeding and ranging behaviour in primates. In: *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes* (Ed. by Clutton-Brock, T. H.), pp. 557-584. London: Academic Press.

Culot, L., Lazo, F. J. J. M., Huynen, M.-C., Poncin, P. & Heymann, E. W. 2010. Seasonal variation in seed dispersal by tamarins alters seed rain in a secondary rainforest. *International Journal of Primatology*, 31, 553-569.

Di Fiore, A. 2003. Ranging behavior and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Yasuní National Park, Ecuador. *American Journal of Primatology,* 59, 47-66.

Doran, D. M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P. & Shah, N. 2002. Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling method. *American Journal of Primatology*, 58, 91-116.

Downs, J. A. 2008. Network analysis of animal space-use patterns. PhD thesis, Florida State University.

Dunbar, R. I. M. 1988. *Primate social systems*. London & Sydney: Croom Helm.

Fashing, P. J., Mulindahabi, F., Gakima, J.-B., Masozera, M., Mununura, I., Plumptre, A. J. & Nguyen, N. 2007. Activity and ranging patterns of *Colobus angolensis ruwenzorii* in Nyungwe Forest, Rwanda: possible costs of large group size. *International Journal of Primatology*, 28, 529-550.

Ferguson, S. H., Taylor, M. K., Born, E. W., Rosing-Asvid, A. & Messier, F. 1999. Determinants of home range size for polar bears (*Ursus maritimus*). *Ecology Letters,* 2, 311-318.

Foerster, S. & Monfort, S. L. 2010. Fecal glucocorticoids as indicators of metabolic stress in female Sykes' monkeys (*Cercopithecus mitis albogularis*). *Hormones and Behavior*, 58, 685-697.

Forest Restoration Research Unit. 2000. Tree seeds and seedlings for restoring forests in Northern Thailand. Biology Department, Science Faculty, Chiang Mai University, Thailand.

Forthman-Quick, D. L. 1986. Activity budgets and the consumption of human food in two troops of baboons, *Papio anubis,* at Gilgil, Kenya. In: *Primate ecology and conservation* (Ed. by G., E. J. & C., L. P.), pp. 221-228. Cambridge: Cambridge University Press.

Garber, P. A. 2000. Evidence for the use of spatial, temporal, and social information by primate foragers. In: *On the move: How and why animals travel in groups* (Ed. by Boinski, S. & Garber, P. A.), pp. 261-297. Chicago and London: The University of Chicago Press.

Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J. & Wilmers, C. C. 2007. LoCoh: nonparameteric kernel methods for constructing home ranges and utilization distributions. *PloS ONE*, e207.

Hamilton, W. J. & Watt, K. E. F. 1970. Refuging. *Annual Review of Ecology and Systematics*, 1, 263-286.

Hanya, G., Kiyono, M., Yamada, A., Suzuki, K., Furukawa, M., Yoshida, Y. & Chijiiwa, A. 2006. Not only annual food abundance but also fallback food quality determines the Japanese macaque density: evidence from seasonal variations in home range size. *Primates*, 47, 275-278.

Harvey, P. H. & Clutton-Brock, T. H. 1981. Primate home-range size and metabolic needs. *Behavioral Ecology and Sociobiology*, 8, 151-155.

Isbell, L. A. 1983. Daily ranging behavior of red colobus (*Colobus badius tephrosceles*) in Kibale Forest, Uganda *Folia primatologica*, 41, 34-48.

Izumiyama, S., Mochizuki, T. & Shiraishi, T. 2003. Troop size, home range area and seasonal range use of the Japanese macaque in the Northern Japan Alps. *Ecological Research*, 18, 465-474.

Janson, C. 2000. Spatial movement strategies: theory, evidence, and challenges. In: *On the move: How and why animals travel in groups* (Ed. by Boinski, S. & Garber, P. A.), pp. 165-203. Chicago: The University of Chicago Press.

Kaplin, B. A. 2001. Ranging behavior of two species of guenons (Cercopithecus lhoesti and C. mitis doggetti) in the Nyungwe Forest Reserve, Rwanda. *International Journal of Primatology*, 22, 521-548.

Lindburg, D. G. 1977. Feeding behaviour and diet of rhesus monkeys (Macaca mulatta) in a Siwalik forest in north India. In: *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes* (Ed. by Clutton-Brock, T. H.), pp. 223-249. London: Academic Press.

Lucas, P. W. & Corlett, R. 1991. Relationship between the diet of *Macaca fascicularis* and forest phenology. *Folia primatologica*, 57, 201-215.

Makwana, S. C. 1978. Field ecology and behaviour of the rhesus macaque (*Macaca mulatta*): I. Group composition, home range, roosting sites, and foraging routes in the Asarori Forest. *Primates*, 19, 483-492.

McLoughlin, P. D. & Ferguson, S. H. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. *Ecoscience*, 7, 123-130.

Milton, K. 1980. *The foraging strategy of howler monkeys: A study in primate economics*. New York: Columbia University Press.

Milton, K. 2000. Quo vadis? Tactics of food search and group movement in primates and other animals. In: *On the move: How and why animals travel in groups* (Ed. by Boinski, S. & Garber, P. A.), pp. 375-417. Chicago and London: The University of Chicago press.

Milton, K. & May, M. L. 1976. Body weight, diet and home range area in primates. *Nature*, 259, 459-462.

Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. New York: John Wiley & Sons.

Naughton-Treves, L., Treves, A., Chapman, C. A. & Wrangham, R. 1998. Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, 35, 596-606.

Olupot, W., Chapman, C. A., Brown, C. H. & Waser, P. M. 1994. Mangabey (*Cercocebus albigena*) population density, group size, and ranging: a twenty-year comparison. *American Journal of Primatology*, 32, 197-205.

Olupot, W., Chapman, C. A., Waser, P. M. & Isabirye-Basuta, G. 1997. Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *American Journal of Primatology*, 43, 65-78.

Phoonjampa, R., Koenig, A., Borries, C., Gale, G. A. & Savini, T. 2010. Selection of Sleeping Trees in Pileated Gibbons (*Hylobates pileatus*). *American Journal of Primatology*, 71, 1-9.

Porter, L. M., Sterr, S. M. & Garber, P. A. 2007. Habitat use and ranging behavior of *Callimico goeldii*. *International Journal of Primatology*, 28, 1035-1058.

Ram, S., Venkatachalam, S. & Sinha, A. 2003. Changing social strategies of wild female bonnet macaques during natural foraging and on provisioning. *Current Science*, 84, 780-790.

Ricklefs, R. E. 1990. *Ecology*, Third edn. New York: W. H. Freeman and Company.

Robbins, M. M. & McNeilage, A. 2003. Home range and frugivory patterns of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology*, 24, 467-491.

Robinson, J. G. 1986. *Seasonal variation in use of time and space by the wedge-capped capuchin monkey,* Cebus olivaceus*: implications for foraging theory*. Washington: Smithsonian Institution Press.

Rodman, P. S. 1979. Skeletal differentiation of *Macaca fascicularis* and *Macaca nemestrina* in relation to arboreal and terrestrial quadrupedalism. *American Journal of Physical Anthropology*, 51, 51-62.

Saj, T., Sicotte, P. & Paterson, J. D. 1999. Influence of human food consumption on the time budget of vervets. *International Journal of Primatology*, 20, 977-994.

Savini, T., Boesch, C. & Reichard, U. H. 2008. Home-range characteristics and the influence of seasonality on female reproduction in white-handed gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand. *American Journal of Physical Anthropology*, 135, 1-12.

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J. & Gitzen, R. A. 1999. Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management*, 63, 739-747.

Seaman, D. E. & Powell, R. A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77, 2075-2085.

Sponsel, L. E., Ruttanadakul, N. & Natadecha-Sponsel, P. 2002. Monkey business? The conservation implications of macaque ethnoprimatology in southern Thailand. In: *Primates face-to-face: Conservation implications of human-nonhuman primate interconnections* (Ed. by Fuentes, A. & Wolfe, L. D.), pp. 288-309. New York: Cambridge University Press.

Stevens, J. R., Rosati, A. G., Ross, K. R. & Hauser, M. D. 2005. Will travel for food: spatial discounting in two new world monkeys. *Current Biology*, 15, 1855-1860.

Struhsaker, T. T. 1975. *The red colobus monkey*. Chicago: University of Chicago Press.

Strum, S. C. 2010. The development of primate raiding: implications for management and conservation. *International Journal of Primatology*, 31, 133-156.

Swedell, L. 2002. Ranging behavior, group size and behavioral flexibility in Ethiopian hamadryas baboons (*Papio hamadryas hamadryas*). *Folia primatologica*, 73, 95-103.

Twinomugisha, D. & Chapman, C. A. 2007. Golden monkey ranging in relation to spatial and temporal variation in food availability. *African Journal of Ecology*, 46, 585-593.

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.

Wheatley, B. P. 1980. Feeding and ranging of East Bornean *Macaca fascicularis*. In: *The macaques: studies in ecology, behavior and evolution* (Ed. by Lindburg, D. G.), pp. 215-246. New York: Van Nostrand Reinhold Company.

Whitaker, D. M., Stauffer, D. F., Norman, G. W., Devers, P. K., Edwards, J., Giuliano, W. M., Harper, C., Igo, W., Sole, J., Spiker, H. & Tefft, B. 2007. Factors associated with variation in home-range size of Appalachian Ruffed Grouse (*Bonasa umbellus*). *The Auk*, 124, 1407-1424.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70, 164-168.

Zabel, C. J., McKelvey, K. & James P. Ward, J. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). *Canadian Journal of Zoology*, 73, 433-439.

Zhao, Q.-K. 1999. Responses to seasonal changes in nutrient quality and patchiness of food in a multigroup community of Tibetan macaques at Mt. Emei. *International Journal of Primatology*, 20, 511-524.

In the previous chapter, we showed that northern pigtailed macaques adapt their ranging behavior to the spatio-temporal variation of fruit availability. Given the impact of human food on macaques' range we wonder if it also has an impact on seed dispersal. In high fruit abundance periods, macaques have a large home range, travel long distances, and eat mainly fruits. Thus human food does not seem to have an impact on seed dispersal. In low fruit abundance period, macaques decrease their home range, travel shorter distances, and eat mainly human food. So this latter could have a big impact on the seed dispersal of some rare fructifying species. However, these species almost all belong to the genus *Ficus* which is eaten by many animal species able to provide good dispersal services.

Moreover, northern pigtailed macaques move where there are more fruits of some species. As highlighted by Tsujino and Yumoto (2009), this behavior may have a positive impact on seed dispersal. During a given period, macaques travel mainly between high concentrations of a given fruiting plant species. Doing so, they disperse this seed species within the specifically suitable habitat in which the con-specific adult trees are distributed, and thus increase the probability of survival of the seeds (Wenny 2001).

~~~

Animal concentration at some places may have a negative impact on seed dispersal (*e.g.* latrines in tapirs, leks in tetras, roosting sites in hornbills or sleeping sites in macaques). The higher defecations' number at these places increases seed density (McConkey 2000; Russo & Augspurger 2004; Schupp et al. 2002) and may strongly decrease seed survival and germination. In the next chapter, we will take advantage from the follow of macaques to study the way they choose their sleeping sites and to discuss what impact this choice could have on their seed dispersal effectiveness.
~~~

CHAPTER 4

Sleeping site selection and pre-sleep behavior in wild pigtailed macaques

Albert, A., Savini, T., Huynen, M.-C. (2011) Sleeping site selection and pre-sleep behavior in wild pigtailed macaques. American Journal of Primatology, 73, 1222-1230.

Résumé

Plusieurs facteurs sont susceptibles de contrôler la sélection des sites dortoirs et les comportements liés au sommeil chez les primates non-humains, parmi lesquels les risques de prédation et la localisation des ressources alimentaires. Nous avons examiné les effets de ces facteurs chez des macaques à queue de cochon du Nord (*Macaca leonina*). Pendant le suivi d'une troupe vivant autour du centre des visiteurs du parc national de Khao Yai (Thaïlande), nous avons enregistré les caractéristiques physiques et la localisation de chaque site et arbre dortoir, la place des individus dans l'arbre, leur posture et leurs comportements. Nous avons collecté des données pour 154 nuits entre avril 2009 et novembre 2010. Les macaques préféraient des arbres hauts (20.9 ± 4.9 m) et de hautes places dortoirs (15.8 ± 4.3 m), ce qui peut être une stratégie anti-prédateur. Le choix de sites dortoirs proches du dernier (146.7 ± 167.9 m) ou du premier (150.4 ± 113.0 m) site alimentaire du jour peut permettre d'économiser de l'énergie et de diminuer les risques de prédation quand les macaques cherchent leur nourriture. De même, le choix de sites dortoirs proches des habitations facilite l'accès à la nourriture humaine lors des périodes de pénurie de fruits. Finalement, le pattern temporel d'utilisation des sites dortoirs, avec une préférence pour quatre des sites dortoirs mais avec peu de réutilisations consécutives, peut être un compromis entre le besoin d'avoir plusieurs sites dortoirs (diminuant ainsi les risque de détection par les prédateurs et les coûts de déplacement vers les sites alimentaires), et le besoin de dormir dans des sites bien connus (garantissant une fuite rapide en cas d'attaque par un prédateur).

Mots-clés**:** évitement de la prédation; ressources alimentaires; parc national de Khao Yai; Thaïlande; *Macaca leonina.*

Abstract

Several factors are likely to control sleeping site selection and pre-sleep behavior in non-human primates, including predation risk and location of food resources. We examined the effects of these factors on the sleeping behavior of northern pigtailed macaques (*Macaca leonina*). While following a troop living in the surroundings of the Visitor Center of Khao Yai National Park (Thailand), we recorded the physical characteristics and location of each sleeping site, tree, the individuals' place in the tree, posture, and behavior. We collected data for 154 nights between April 2009 and November 2010. The monkeys preferred tall sleeping trees (20.9 ± 4.9 m) and high sleeping places (15.8 ± 4.3 m), which may be an anti-predator strategy. The choice of sleeping trees close to the last (146.7 ± 167.9 m) or to the first (150.4 ± 113.0 m) feeding tree of the day may save energy and decrease predation risk when monkeys are searching for food. Similarly, the choice of sleeping sites close to human settlements eases the access to human food during periods of fruit scarcity. Finally, the temporal pattern of use of sleeping sites, with a preference for four of the sleeping sites but few reuses during consecutive nights, may be a trade-off between the need to have several sleeping sites (decreasing detection by predators and travel costs to feeding sites), and the need to sleep in well-known sites (guaranteeing a faster escape in case of predator attack).

Key words**:** predation avoidance; food resources; Khao Yai National Park; Thailand; *Macaca leonina.*

Introduction

Like many traits subject to natural selection, sleeping behavior is likely affected by several factors, either biotic, such as the influence of competitors, predators or parasites, or abiotic, such as the weather (Anderson 1984). Many studies of sleeping behavior have highlighted the importance of predation pressure in primate sleeping site selection (*e.g.* Caine 1987; Day & Elwood 1999; Hamilton 1982; Matsuda et al. 2008; Reichard 1998; Smith et al. 2008; Tenaza & Tilson 1985; von Hippel 1998). Indeed, primates spend about half of their life sleeping and their greater vulnerability when they sleep explains why sleeping sites should be selected with care. Several reports of attacks at sleeping sites have confirmed nocturnal exposure to predation (Altmann & Altmann 1970; Busse 1980), and one could expect species facing high predation risk to select sites offering high safety guarantees. Several studies have also emphasized the importance of food resource proximity for sleeping site choice (*e.g.* multiple central place foraging hypothesis or MCPF) (Anderson 1998; Chapman 1989; Chapman et al. 1989; Day & Elwood 1999; Fan & Jiang 2008; Heymann 1995; Mendes Pontes & Soares 2005; Phoonjampa et al. 2010; Smith et al. 2007; Sugardjito 1983; Vessey 1973; von Hippel 1998).

During our long-term field study of the feeding ecology of northern pigtailed macaques (*Macaca leonina;* Blyth, 1863), we collected data on a habituated troop's sleeping habits. Northern pigtailed macaques form multi-male multi-female troops and have a high degree of sexual dimorphism (males range from 6.2 to 14.5 kg and females from 4.7 to 10.9 kg). Like many other cercopithecine species, they are semi-terrestrial (members of the HQ troop were on the ground for 60% of the 21,377 scans of a single animal (Albert, unpublished data)), frugivorous and their cheek pouches enable them to store fruits. Although few data are available for this species, we know that a closely related species, *M. nemestrina*, forms troops ranging from nine to 81 individuals (Oi 1990).

We describe the physical characteristics and locations of sleeping trees selected by the troop, and examine this selection based on the two main hypotheses available in the literature. Following the anti-predation hypothesis we predicted that macaques should travel quietly to their sleeping site and should prefer tall trees, which may be a strategy to avoid ground predators (Di Bitetti et al. 2000; Fan & Jiang 2008; Li et al. 2006; von Hippel 1998). Moreover they should prefer trees with an open crown (*i.e.* low proportion of leaf cover), through which they can easily see the approaching bird or arboreal predator, and they should avoid trees supporting lianas which can allow a predator to climb and access the sleeping places. In addition, we expected a regular change of their sleeping sites to prevent a predator from learning about reuse of sleeping sites. Lastly, we expected macaques to choose trees in particular locations making the site safer, such as near a river as shown in several species of primates, including pigtailed macaques (Matsuda et al. 2008; Matsuda et al. 2011). Following the MCPF hypothesis, we predicted that the sleeping sites, as central places, should be close to the last or first feeding tree of the day to minimize travel costs. In addition to these predictions, we expected pigtailed macaques, like most diurnal primates (Anderson 2000), to model the variation in the length of their daily activities based on the variation in the photoperiod.

Methods

Study site

This study was conducted at Khao Yai National Park (KYNP; 2,168 km²; 14° 05'–15'N, 101° 05'–50'E). The study site is located around the park Visitor Center, an area of seasonally wet evergreen forest (Forest Restoration Research Unit 2000) at 700-800 m ASL and including a ranger station and various tourist facilities. The climate is monsoonal with a wet season (from May to October) and a relatively dry season divided into a cool (from November to February) and a hot (from March to April) period. The mean monthly temperature ranges from 19°C (December, January) to 24°C (March, April) and the annual precipitation averages 2,504 mm with monthly averages of 69 mm in the dry season and 353 mm in the wet season (2006-2009).

Among the few predator species present on the study site, the clouded leopard (*Neofelis nebulosa*), a nocturnal arboreal cat, and pythons (*Python reticulatus* and *P. molurus*) pose the major threats (Khamcha & Sukumal 2009). Pythons are diurnal, but macaques are extremely vigilant to predators while in low forest strata during day time and ready to climb into the trees in case of danger. Encounters with pythons have often been witnessed by the observer (A.A.) and always elicited macaque mobbing behavior, screaming, shaking of branches and jumping fast and close to the snake (Albert, unpublished data). Davies (1990) reported the presence of a clouded leopard in a KYNP pigtailed macaque sleeping site. The predator's reaction to the observer's approach made it conspicuous and induced alarm calls by the macaques. The terrestrial Asian golden cat (*Felis temminckii*), and birds of prey such as the mountain hawk eagle (*Spizaetus nipalensis*) and crested serpent eagles (*Spilornis cheela*) are less likely to represent a threat (Fam & Nijman 2011); birds of prey pose a threat mainly during the day.

Study group

The study troop (HQ troop) included 32 to 39 individuals: 2 to 3 adult males, 12 to 13 adult females, 17 to 20 juveniles and 1 to 3 sub-adult males. Their diet varied according to season. During the rainy season they mainly ate fruits (51% of 1,012 feeding observations compared to 22% of 843 feeding observations during the dry season). During the dry season they mainly ate human food (44% compared to 12% in rainy season). Human food was available year-round: the macaques either stole it from houses or trash cans, or begged from tourists. They completed their diet with flowers, non-reproductive plant parts, invertebrates, small vertebrates and fungi (Chapter 2 and 3).

Data collection

In this paper, we used the following terminology: "*sleeping tree*" is the tree in which macaques stayed overnight; "*sleeping site*" is the location of sleeping trees in the home range; "*sleeping place*" is the location of an individual in a sleeping tree; "*pre-sleep behavior*" summarizes the behavioral pattern associated with the choice of sleeping trees and sleeping places; "*shared sleeping tree*" indicates a sleeping tree simultaneously used by several individuals (Anderson 1984; Reichard 1998); "*sleeping posture*" refers to the body orientation at the sleeping place (*e.g.* sitting, lying). Finally, "*preferred sleeping sites*" are the sites frequently selected (each one > 10% of nights).

A.A. collected all field data. She followed the study troop for 1029 hours, and for logistical reasons, divided the study in three periods (April - July 2009 [Period 1]: 370 h; December 2009 - March 2010 [Period 2]: 288 h; August - October 2010 [Period 3]: 371 h). As the study was conducted in parallel with a study of seed dispersal, she followed the macaques for one day every two or three days, for an average of 7.25 days per month, and covering 19 days on average per month. She usually found the macaques 15 to 30 minutes before dawn, and then followed them all day until they reached the next sleeping site. As she did not follow them on two consecutive days, she could not see them entering a site on a given evening and exiting this same site on the next morning. Every 30 minutes, A.A. estimated the height of all visible macaques. Occasionally, the troop used two adjacent sleeping sites but we considered only the sleeping site sheltering the biggest proportion of the troop in the analysis. A.A. noted the troop's locations based on GPS coordinates automatically recorded every 30 minutes to maximize independence between two consecutive points (Phoonjampa et al. 2010), for an average of 182 GPS positions per month. The GPS errors ranged from 6 to 10 m. We calculated monthly home range sizes using 95% kernels and the core areas using 50% kernels with ArcView 3.2a (ESRI). The GPS coordinates of sleeping sites and all fruiting trees were used to measure the distance between the sleeping sites and the last or first feeding tree of the day.

A.A. collected *ad libitum* data on the behavior of each individual present in a sleeping site, its sleeping place and posture (sitting, lying, *etc.*) in the tree and on the branches. She noted the time of exit from and/or entry into the sleeping site for each night. For each sleeping site, A.A. recorded the species, the diameter at breast height (DBH), whether the tree had a lower or equal height to the canopy or whether it was emergent. She also estimated its total height (to the nearest meter up to 10 m and then to the nearest 2 m), along with the height of the lowest branches and the crown diameter, and she also noted the sleeping place of every visible macaque within the tree. Trees of DBH ≥ 40 cm were considered as large.

We defined a 5-point scale index to quantify the proportion of leaf and resulting visibility of the ground and of the sky from the macaques' locations. A.A. scored visibility from 0 (very high visibility, no leaf coverage), to 1 (high visibility, 1- 25 % leaf coverage), 2 (medium visibility, 26-50 % leaf coverage), 3 (low visibility, 51-75 % leaf coverage), and 4 (no visibility, 76-100 % leaf coverage). She also noted the presence/absence of lianas on the tree trunks and the distance between each sleeping site and the river and human settlements. In addition, she established across the entire macaque home range twelve north–south botanical transects, twenty meters wide and approximately 110 meters apart, covering 27 ha, *i.e.* approximately 20% of the study area (Mueller-Dombois & Ellenberg 1974; Struhsaker 1975). A.A. measured, tagged, mapped, and identified to species all trees of DBH ≥ 10 cm. This enabled us to evaluate the spatial distribution and abundance of plant species in the troop's home range. We conducted phenology on a sample of about 10 trees per species, located in the nearby long-term biodiversity plot (Brockelman 1998).

Data analysis

We performed 2-tailed statistical tests with Statistica 9.0 (α level: 0.05). To analyze the reuse of sleeping sites we counted the number of times the same sleeping site was used for two consecutive nights. We calculated the binomial probability of having the same proportion of trees with a DBH ≥ 40 cm (*i.e.* large trees) among the sleeping and non-sleeping trees across the home range, and, for each month, we calculated the binomial probabilities of having the same number of nights spent in the core area as expected according to the relative sizes of the core and peripheral areas. We performed a Mann–Whitney *U*-test to compare the height of the macaques' average place in the canopy between days and nights. To test the multiple central place foraging (MCPF) theory (Chapman et al.1989), we compared, for each event of sleeping site selection, the distance between the feeding tree (last and/or first of the day) and (1) the chosen sleeping site (*i.e.* observed distance), (2) the nearest sleeping site (*i.e.* distance if they use a MCPF strategy or MCPF 1), (3) the nearest preferred (selected more than 10% of nights) sleeping site (*i.e.* distance if they use a modified MCPF strategy or MCPF 2), and (4) the mean sleeping site, calculated from the arithmetic mean of the GPS coordinates of all sleeping sites (*i.e.* estimated distance if they use a central place foraging strategy or CPF). We conducted pair-wise tests using Wilcoxon signed rank tests to analyze the distances between the sleeping and feeding sites for each strategy tested (Observed *vs* MCPF 1; Observed *vs* MCPF 2; Observed *vs* CPF). Finally, we performed Spearman correlations to relate the times of entry in and exit from sleeping sites with the times of sunset and sunrise. The present study was approved by the Department of National Parks, Wildlife, and Plant Conservation, Bangkok, conducted in full compliance with the laws of the Kingdom of Thailand, and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

Results

We observed the macaques at sleeping sites 154 times, including 70 occasions when they were leaving the site in the morning (*i.e.* 77% of days macaques were followed) and 84 when they were entering the site in the evening (*i.e.* 93% of days).

Characteristics of sleeping sites and sleeping trees

The macaques used sixteen sleeping sites during the study period (Figure 4.1), but the accumulation curve of the number of these sleeping sites over the study period did not reach an asymptote (Figure 4.2). The macaques reused fourteen sleeping sites (range: 2-36 times) with a clear preference for four of them used for more than two thirds (71%) of the total number of nights. Other troops of pigtailed macaques used at least two of the study troop's sleeping sites, but never simultaneously. Of the 101 occasions where the sleeping site of the previous night was known, the macaques used the same sleeping site 22 times (22%). Use on two consecutive nights occurred 19 times and four consecutive nights occurred only once. The consecutive reuses concerned mainly the four preferred sleeping sites (96% of consecutive nights).

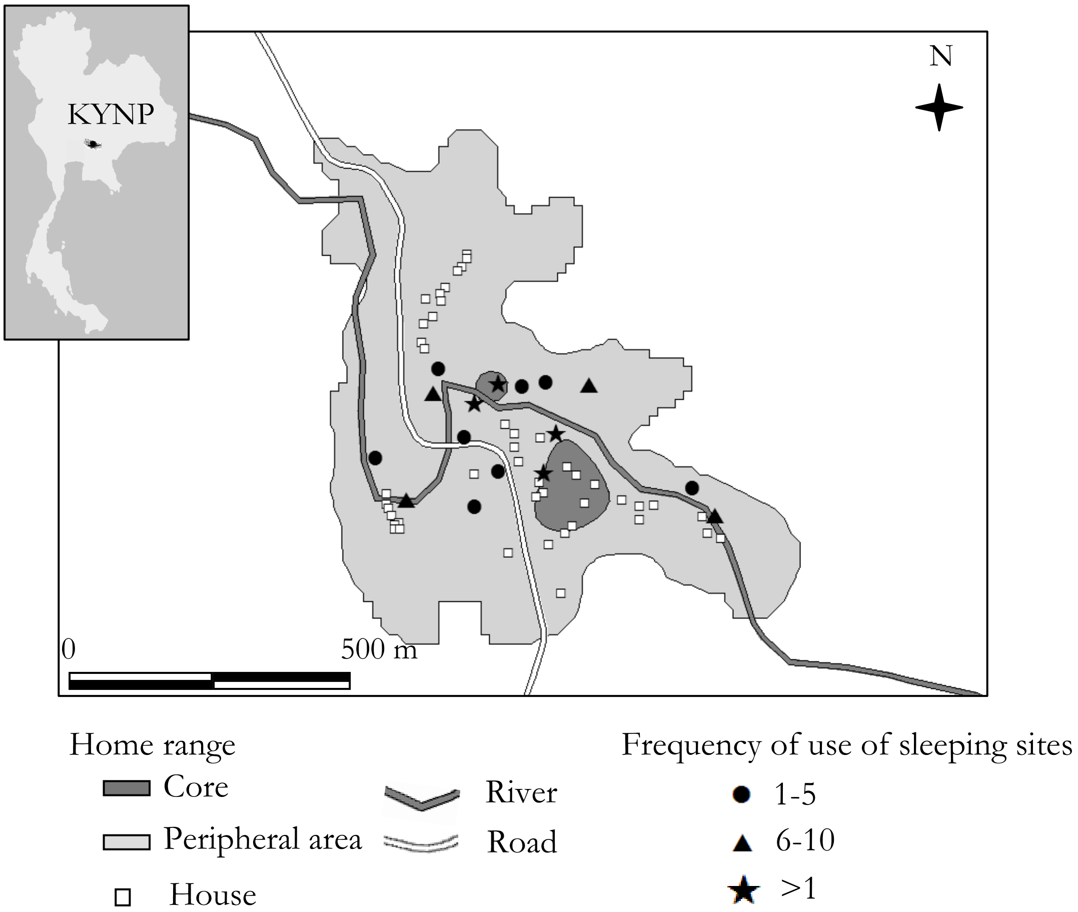


Figure 4.1. Yearly home range (core area (50% kernel) and peripheral area (95% kernel)), and location and frequency of use of sleeping sites.

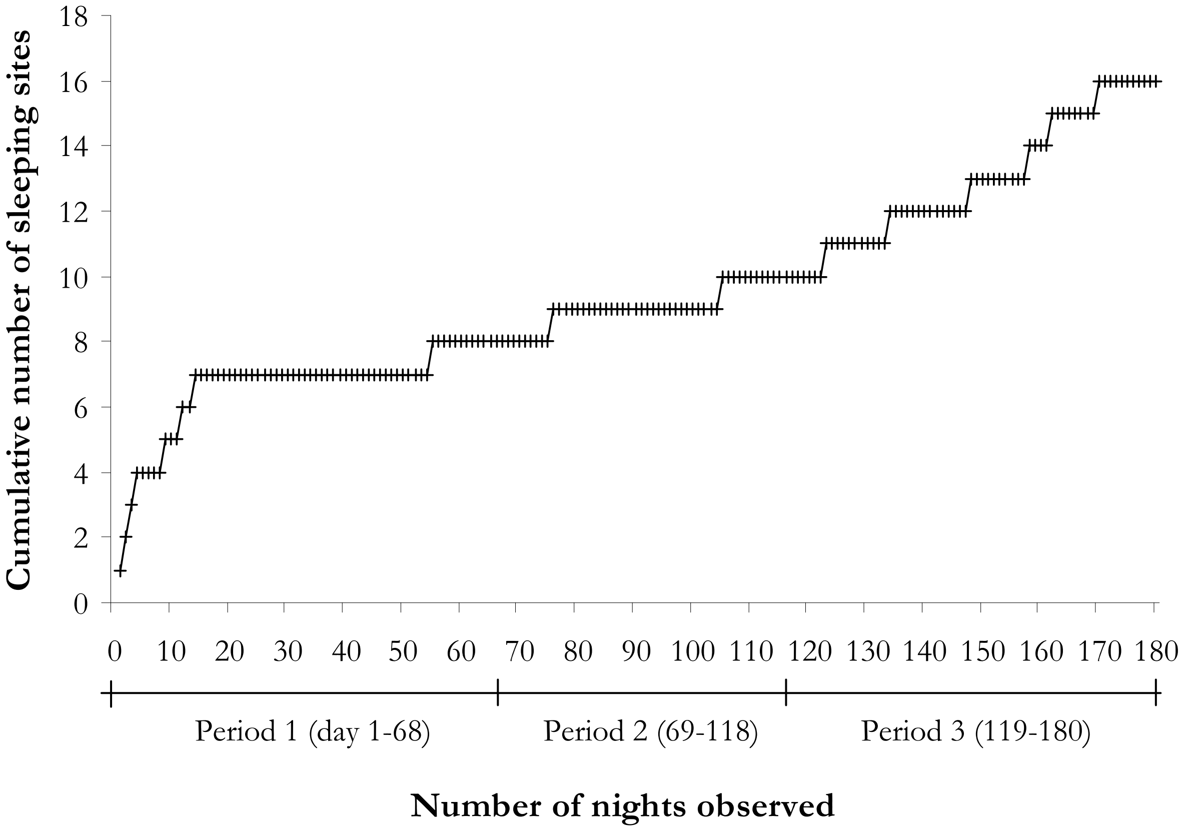


Figure 4.2. Cumulative number of new sleeping sites used by the HQ troop according to the number of nights observed.

Each sleeping site included one to eight identified sleeping trees (mean = 4.3), for a total of 47 sleeping trees. Every sleeping tree was shared between troop members. The only purpose of the sleeping trees was overnight stay, except for two trees (a *Ficus virens* tree (Moraceae) and an *Antiaris toxicaria* tree (Moraceae)) which fruited repeatedly over the study and which macaques used for sleeping and feeding during the same night. Among the 229 tree species measured on the botanical transects, the macaques used 29 species as sleeping trees.

The physical characteristics of sleeping trees corresponded to a general pattern (Table 4.1). The trees of DBH ≥ 40 cm were more often used than expected (Binomial probability: $P < 0.001$). The crowns of sleeping trees were mostly of similar height as adjacent trees ($N = 47$, 83%), and connected to their branches ($N = 47$, 92%). Few sleeping trees supported lianas on their trunks ($N = 47$, 13%). Above the animals, the leaves provided moderate cover (*i.e.* 26-50 %). The visibility of the animals from the ground was high (*i.e.* 1-25 %). The observer often saw the macaques using the canopy or lianas connecting the adjacent trees to access the sleeping tree but rarely going there directly from the trunk base.

Table 4.1. Physical characteristics (mean ± SD) of the identified sleeping trees used by the HQ troop.

Sleeping site ID	No known trees	DBH (cm)	Height (m)	Height of lowest branch (m)	Crown diameter (m)	Leaf cover	Visibility from the ground	Height of sleeping place (m)
01*	6	93.3±34.7	23.0±3.6	9.7±4.2	13.0±3.7	2.8±1.0	2.8±1.0	16.8±3.8
02*	8	49.0±25.2	21.5±7.7	12.8±7.2	8.4±3.8	2.1±1.1	1.4±1.1	17.6±6.3
03*	4	51.1±23.3	25.0±0.8	12.3±3.3	8.8±2.2	1.8±1.0	1.1±0.0	20.0±2.8
04*	6	38.7±27.2	22.7±3.8	11.7±2.1	9.0±7.4	2.0±1.4	0;8±0.8	16.3±2.3
05*	2	42.5±14.8	18.0±2.8	5.5±0.7	10.0±0.0	1.0±1.4	0.5±0.7	15.5±2.1
06*	5	47.4±15.3	18.2±4.8	8.8±4.8	8.6±2.5	2.8±0.4	1.0±0.0	14.0±4.7
08*	5	62.0±10.0	16.8±1.9	3.8±1.3	9.4±1.9	1.6±0.5	0.4±0.5	12.4±1.7
09*	1	60.0±0.0	18.0±0.0	5.0±0.0	20.0±0.0	2.0±0.0	1.0±0.0	12.0±0.0
11*	3	65.5±9.5	23.3±1.2	4.3±1.5	12.0±0.0	2.3±1.2	2.0±1.0	16.0±1.0
13	4	56.3±28.0	21.5±5.7	6.8±2.5	15.3±6.7	2.5±1.0	1.8±1.0	15.3±4.7
15*	3	39.3±10.1	17.7±1.5	6.3±2.1	12.3±4.0	8.3±0.6	2.0±1.7	0.0±0.0
Total	47	55.7±26.7	20.9±4.9	8.9±4.9	10.3±4.6	2.2±1.1	1.3±1.1	15.8±4.3
(tree range)	(1-8)	(13.3-139.0)	(12.0-35.0)	(2.0-25.0)	(2.0-25.0)	(0.0-4.0)	(0.0-4.0)	(8.0-30.0)

* Reused sleeping sites

Spatial distribution of sleeping sites

We calculated monthly home range size based on troop location GPS points (mean = 182.3 ± 27.1 GPS points per month; range: 119-226). Over the study period, the monthly home range varied from 6 ha (January 2010) to 73 ha (September 2010) and the size of the core area from less than 1 ha (January 2010) to 11 ha (September 2010). For 10 of 12 months, the accumulation curve of the home range size reached an asymptote.

The proportion of nights spent in the core area varied greatly according to months, from 0% (December, January and February 2010) to 100% (June 2009). For eight months, this proportion was significantly higher than the expected number of nights spent in this zone (Binomial probabilities; Figure 4.3).

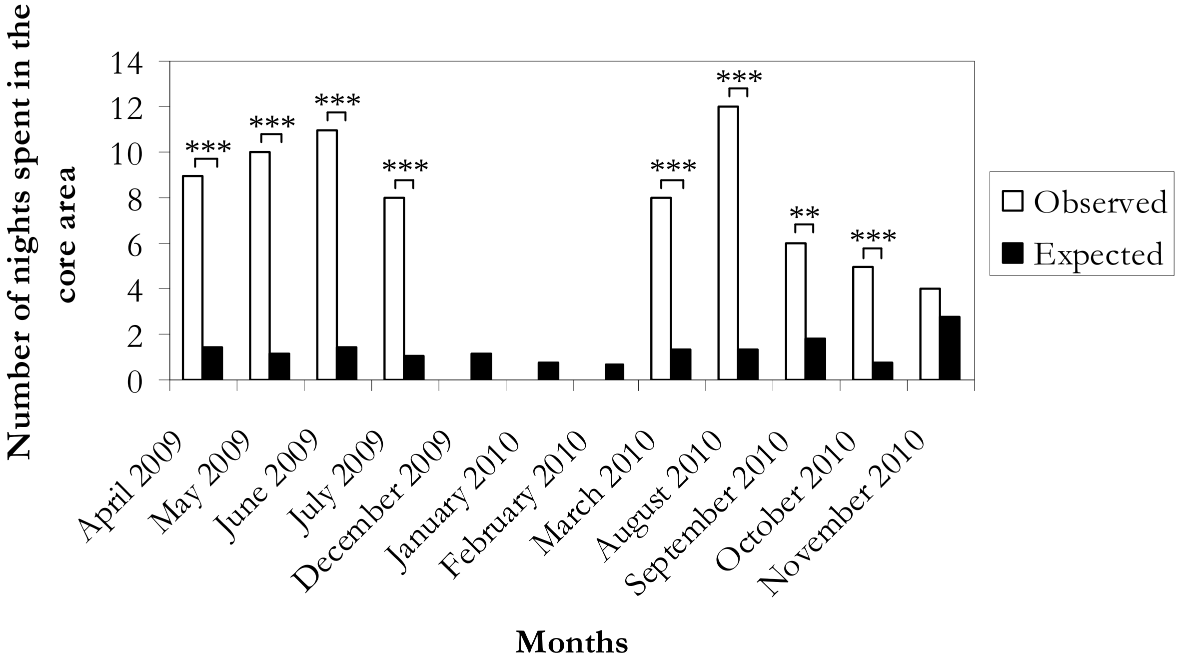


Figure 4.3. Number of nights macaques were observed sleeping in the core area compared with the numbers expected in this area according to the relative sizes of the core area and the peripheral area (Binomial probabilities). *** $P < 0.001$; ** $P < 0.005$

Twelve of the 16 sleeping sites were on the river bank (75%) and four (25%) at an average distance of 88.8 ± 48.7 m from the river. Six of the 16 sleeping sites (38%) were contiguous with human settlements and ten (63%) were at an average distance of 62.9 ± 32.2 m from human settlements. The sleeping site chosen by the troop was an average distance of 146.7 ± 167.9 m (*N* = 74, range: 0-647 m) from the last feeding tree of the evening, and 150.4

± 113.0 m from the first feeding tree of the following morning ($N = 63$, range: 0-427 m). The macaques chose the nearest sleeping site to the last/first feeding tree on 57 nights (42%) and the nearest sleeping site among the preferred sleeping sites on 62 nights (45%). The travel distance from the feeding tree to the chosen sleeping site was about 25% less than to the mean sleeping site (148.4 m *vs* 202.2 m; Wilcoxon signed ranks test: $Z = 6.26$, $N = 137$, $P < 0.001$) and almost double the distance to the nearest sleeping site (148.4 m *vs* 83.7 m; Wilcoxon signed ranks test: $Z = 7.72$, $N = 137$, $P < 0.001$) (Figure 4.4). However, there was no significant difference between the distance from the feeding tree to the chosen sleeping site and the distance to the nearest and preferred sleeping sites (Wilcoxon signed ranks test: $Z = 1.96$, $N = 137$, $P = 0.050$).

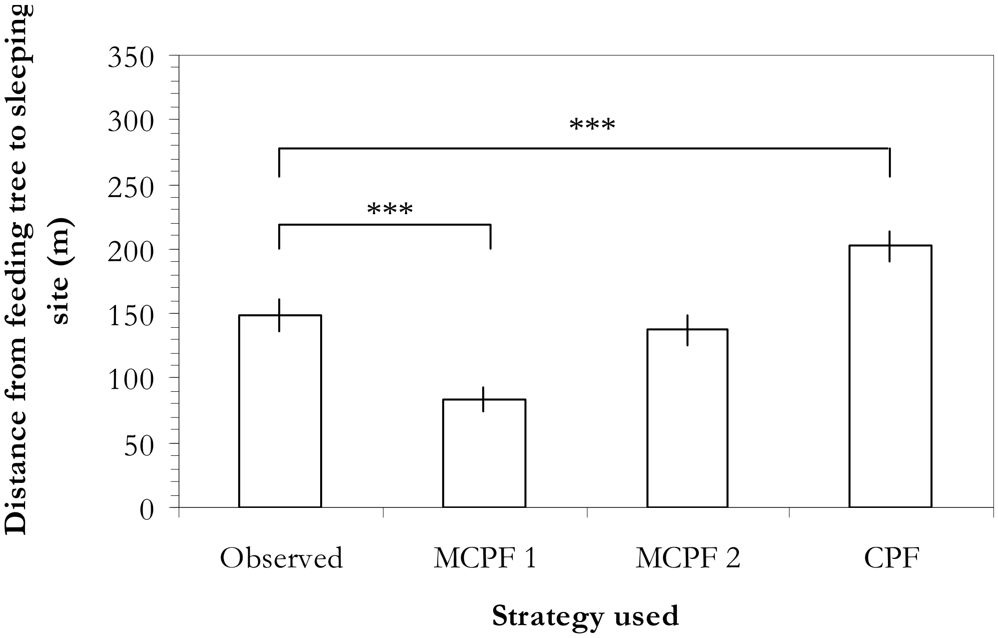


Figure 4.4. Mean (± SE) distances between the last/first feeding tree of the day and the observed sleeping site (Observed), the nearest sleeping site (MCPF 1), the nearest preferred sleeping site (MCPF 2), and the mean sleeping site (CPF). *** P < 0.001

Sleeping place and posture

Pigtailed macaques always slept in a sitting posture, on intermediate and terminal branches, never near the trunk, and usually in the mid- and upper part of the trees. They often shared sleeping places forming huddling groups including two to five individuals, usually one or several females and her/their infants and juveniles. Macaques stayed higher during the night than during the day (mean = 2.2 ± 1.2 (day) *vs* 16.0 ± 3.1 (night)).

Times of entry to and exit from sleeping sites

The study troop members did not enter or exit a sleeping site simultaneously but their average time for leaving was 06h05 ± 18 min ($N = 43$, range: 05h30-07h15), and for entering 18h16 ± 27 min ($N = 84$, range: 17h30-19h00). Thus, macaques spent an average of 11h55 ± 43 min ($N = 127$, range: 10h49-12h37) in their sleeping sites. The times of entry and exit from sleeping sites were highly correlated with the times of sunset and sunrise (Spearman correlation: sunrise: $r_S = 0.73$, $N = 42$, $P < 0.001$; sunset: $r_S = 0.74$, $N = 84$, $P < 0.001$). The troop adult males were often the first members to leave the sleeping trees in the morning.

Encounters with neighboring troops

Encounters with other troops of pigtailed macaques in the home range occurred nine times during the 1029 hours of observation, including twice in the core area, six times near the edge and once in-between. These encounters were always agonistic, and included direct attacks.

Discussion

During the study period, pigtailed macaques used sleeping sites mainly located in the core of their home range, close to the river and to human settlements. The troop clearly preferred four sleeping sites which they used very frequently, although they usually avoided sleeping in the same site on consecutive nights. Pigtailed macaques preferred trees bigger than the average, but not necessarily taller, and favored large crowns, allowing greater visibility to the ground, and which were connected to the adjacent canopy. They often chose the nearest site to the last or first feeding tree of the day. The time the troop entered and exited the sleeping site was significantly correlated with the time of sunset and sunrise. These results suggest that sleeping site selection by northern pigtailed macaques follows the predictions of both hypotheses of predation avoidance and MCPF.

Predation

The tendency for pigtailed macaques to use the ground or low forest strata during the day (Albert, unpublished data) might have led to some expectation that they would behave similarly during the night. That they sleep higher in the canopy indicates different constraints between days and nights, likely explained by predation avoidance as suggested by others (Chapman 1989; Day & Elwood 1999; Di Bitetti et al. 2000; Fan & Jiang 2008; Li et al. 2006; Liu & Zhao 2004; Phoonjampa et al. 2010; Reichard 1998; Tenaza & Tilson 1985; von Hippel 1998).

The study troop preference for sleeping trees with a crown of equal height and connected to the adjacent trees also suggests predator avoidance, as it provides more escape routes than emergent trees. This strategy is somewhat unusual but has been reported previously for black crested gibbons (Fan & Jiang 2008) and proboscis monkeys (Matsuda et al. 2008).

The troop adult males were often the first members to leave the sleeping trees in the morning, a pattern Anderson and McGrew (1984) interpreted as lowering the likelihood of attack to the most vulnerable members of the troop, *i.e.* females or juveniles, by a predator waiting near the sleeping trees. As predicted, few sleeping trees had lianas on their trunks, making it more difficult for a predator to climb and access the sleeping places, which again could be considered as an anti-predator strategy (Phoonjampa et al. 2010; Tenaza & Tilson 1985).

The choice of sleeping sites located near the river is puzzling as the study troop members rarely drank from the river. This choice may reflect an anti-predator strategy, as suggested for proboscis monkeys (Matsuda et al. 2008; Matsuda et al. 2011). The presence of the river along one side of the sleeping site decreases the area of ground needing monitoring and also lowers the probability of being surprised by a predator approaching from the ground.

The continuous increase in number of sleeping sites with the duration of the study suggests that macaques changed regularly their location and sometimes abandon some sleeping sites to select new ones. This could decrease the probability that predators predict the location of sleeping sites (Day & Elwood 1999; Fan & Jiang 2008; Heymann 1995; Li et al. 2006; Phoonjampa et al. 2010; Reichard 1998; Smith et al. 2007). This pattern of diversification and reuse of sleeping sites may reflect a trade-off between two exclusive security strategies. Macaques would tend to change regularly their sleeping sites to decrease detection by predators, but would prefer to stay in a few sites they know well enough to escape safely in case of predator attack (Chapman 1989; Day & Elwood 1999; Di Bitetti et al. 2000). The low number of sleeping trees found in this troop (47 sleeping trees used in 154 nights) compared to other primate species living in the same area (*e.g. Hylobates pileatus* used 170 sleeping trees in 113 nights (Phoonjampa et al. 2010)) may be explained in several ways. First the number of macaque sleeping trees might have been underestimated because they were difficult to see in the dark, and only the identified trees were analyzed for the study. Second the higher probability of reuse of some sleeping trees by macaques may point to a different probability of predation for each species. Gibbons, usually living farther from the human settlements, may be more subject to predation and thus may need to change more often the location of their sleeping trees.

Finally, the preference for crowns offering greater visibility of the ground highlights the need for macaques to monitor the surroundings below. Thus predation from the ground seems either to still exist or to have disappeared too recently to have changed the macaques' anti-predator strategies. The preference for open crowns has already been described in *Macaca fascicularis* (Kurland 1973) and *Macaca arctoides* (Estrada and Estrada 1976). The authors considered this as an adaptive choice providing better visibility of potential predators.

Food resources

Sleeping sites tended to be equidistant from the last feeding tree of the day and from the first feeding tree of the next morning. Following our predictions, the ranging pattern of the HQ troop seems to correspond to the definition of the multiple central place foraging (MCPF) strategy suggested by Chapman *et al.* (1989). Indeed, pigtailed macaques describe daily round-trips between a limited number of central places and other points of their home range corresponding mainly to food sources (Caldecott 1986). However, we also observed a slight difference between the strategy of our troop and the predictions from the MCPF hypothesis: macaques chose the nearest sleeping site to the last/first feeding tree (as suggested by the MCPF hypothesis), but mainly if this nearest site was one of their preferred sleeping sites (differing from the MCPF hypothesis). This could be a trade-off between the need to have several sleeping sites decreasing the travel costs to feeding sites and the need to use sleeping sites with characteristics pertinent to protection against predators. Their choice would be therefore maximizing security while minimizing energetic costs.

The lack of an asymptote for the accumulation curve of sleeping sites during the observation period indicates that the maximum number of available sleeping sites has not yet been reached and we can expect the number of sleeping sites to increase with additional observations. Indeed the seasonal variation in the home range location, probably caused by variation in resource distribution (Chapter 3), could cause variation in the use of sleeping sites.

Beyond the anti-predator strategy, the choice of the Visitor Center zone as sleeping sites area could be explained by the presence of human food. During the dry season, macaques face the scarcity of fruiting trees (Chapter 3). They have to compensate with other food resources (fallback food) such as leaves, fungus or invertebrates. The HQ troop has shown a preference for human food as fallback food (Chapter 2 and 3).

Photoperiod

The daily activities of the study troop seemed to follow the variation in the photoperiod. The times of entry and exit from sleeping sites are highly correlated with sunset and sunrise. The same correlation pattern is present in most diurnal primate species (reviewed by Anderson 2000), however with some inter-specific variation in the correspondence between the time of entry in the sleeping site and the time of sunset. *Saguinus fuscicollis* and *S. mystax* enter their sleeping sites before sunset, between 15h46 and 16h12 (Smith et al. 2007), while *Hylobates pileatus* and *H. lar* enter theirs even much earlier, between 11h00 and 17h00 (Phoonjampa et al. 2010; Reichard 1998). The variation in the time animal entered the sleeping site corresponds to the variation in daily activity patterns probably resulting from different foraging strategies (Anderson 2000). Thus pigtailed macaques seem to exploit their feeding resources as long as possible before going to sleep.

Three other factors influencing the selection of sleeping sites have already been described in the literature: interactions with conspecifics, parasite avoidance and need for comfort. First, most primate species are highly social and prefer to stay in physical or at least visual contact at sleeping sites (Anderson 1998). However, they might also try to avoid neighboring conspecific groups (Anderson 1998; Di Bitetti et al. 2000; Heymann 1995; Li et al. 2006; Phoonjampa et al. 2010; Reichard 1998; Smith et al. 2007; von Hippel 1998). The troop preference for sleeping trees with large crowns may also reflect a need for group cohesion during the night. The troop's frequent choice of sleeping sites within the home range core area may decrease the probability of agonistic encounters with other troops at sleeping sites.

Second, in yellow baboons for example, the low reuse frequency of sleeping sites also seen in our troop has been linked to a behavioral strategy of parasite avoidance (Hausfater and Maede 1982). Moreover, the troop's usual avoidance of the ground below the sleeping trees for entry or exit might decrease the probability of endoparasite re-infestation by contact with their own feces within or near the sleeping site. Only a study focusing on parasite load estimation would enable us to confirm the potential presence of a parasite avoidance strategy.

Third, similar to many primate species and all macaques and baboons, pigtailed macaques form clusters at sleeping sites (Anderson 2000). Some authors have suggested these clusters could function as part of an anti-predator strategy or represent an adaptation for reducing heat loss during the night (Anderson 1998; Anderson 2000; Fan & Jiang 2008; Zhang 1995). Our data did not allow testing of the correlation between cluster formation and temperature. Further studies are needed to specifically test these various hypotheses.

This study concerns only a single troop of pigtailed macaques, whose home range is characterized by a close proximity to human settlements. The study of other troops, living in more remote areas, will be needed to obtain a more comprehensive understanding of sleeping site selection and associated behaviors in *Macaca leonina*.

Acknowledgments

We thank the Department of National Park, Wildlife and Plant Conservation and the National Research Council of Thailand for granting research permission, and the superintendent of Khao Yai National Park for his hospitality. We thank George Gale, Rungnapa Phoonjampa, and Dusit Ngoprasert for their help. We are grateful to Carola Borries, Paul A. Garber, and two anonymous reviewers for their helpful comments on the manuscript. This study was carried out with the financial support from the University of Liège, Belgium (A.A), and of the Biodiversity Research and Training Program, Thailand (Grant No. BRT R_349007) (T.S. and M-C.H.). The research was conducted in full compliance with the laws of the Kingdom of Thailand, and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

Literature cited

Altmann, S. A. & Altmann, J. 1970. *Baboon ecology: African field research*. Basel: Karger.

Anderson, J. R. 1984. Ethology and ecology of sleep in monkeys and apes. *Advances in the Study of Behavior*, 14, 156-229.

Anderson, J. R. 1998. Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *American Journal of Primatology,* 46, 63-75.

Anderson, J. R. 2000. Sleep-related behavioural adaptations in free-ranging anthropoid primates. *Sleep Medicine Reviews*, 4, 355-373.

Anderson, J. R. & McGrew, W. C. 1984. Guinea baboons (*Papio papio*) at a sleeping site. *American Journal of Primatology*, 6, 1-14.

Brockelman, W. Y. 1998. Long term ecological research plot for the study of animals diets in Khao Yai National Park. In: *The Asian Hornbills: Ecology and Conservation. Thai Studies in Biodiversity 2* (Ed. by Poonsawad, P.), pp. 307-310. Bangkok: Biodiversity Research and Training Program, National Center for Genetic Engineering and Biotechnology with support from the Thailand Research Fund in collaboration with Science Society of Thailand.

Busse, C. 1980. Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve. *Botswana Notes and Records*, 12, 15-21.

Caine, N. G. 1987. Vigilance, vocalizations, and cryptic behavior at retirement in captive groups of red-bellied tamarins (*Saguinus labiatus*). *American Journal of Primatology*, 12, 241-250.

Caldecott, J. O. 1986. *An ecological and behavioural study of the pig-tailed macaque*. Basel: Karger.

Chapman, C. A. 1989. Spider monkey sleeping sites: Use and availability. *American Journal of Primatology*, 18, 53-60.

Chapman, C. A., Chapman, L. J. & McLaughlin, R. L. 1989. Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. *Oecologia*, 79, 506-511.

Davies, R. G. 1990. Sighting of a clouded leopard (*Neofelis nebulosa*) in a troop of pigtail macaques (*Macaca nemestrina*) in Khao Yai National Park, Thailand. *Natural History Bulletin of the Siam Society*, 28, 95-96.

Day, R. T. & Elwood, R. W. 1999. Sleeping site selection by the golden-handed tamarin *Saguinus midas midas*: the role of predation risks, proximity to feeding sites, and territorial defence. . *Ethology*, 105, 1035-1051.

Di Bitetti, M. S., Vidal, E. M. L., Baldovino, M. C. & Benesovsky, V. 2000. Sleeping site preferences in tufted capuchin monkeys (*Cebus apella nigritus*). *American Journal of Primatology*, 50, 257-274.

Estrada, A. & Estrada, R. 1976. Establishment of a free-ranging colony of stumptail macaques (*Macaca arctoides*): relations to the ecology. *Primates*, 17, 337-355.

Fam, S. D. & Nijman, V. 2011. *Spizaetus* hawk-eagles as predators of arboreal colobines. *Primates*, 52, 105-110.

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, 153-160.

Forest Restoration Research Unit. 2000. Tree seeds and seedlings for restoring forests in Northern Thailand. Biology Department, Science Faculty, Chiang Mai University, Thailand.

Hamilton, W. J. 1982. Baboon sleeping site preferences and relationships to primate grouping patterns. *American Journal of Primatology*, 3, 41-53.

Hausfater, G. & Maede, B. J. 1982. Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates*, 23, 287-297.

Heymann, E. W. 1995. Sleeping habits of tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Mammalia, Primates, Callitrichidae), in north-eastern Peru. *Journal of Zoology*, 237, 211-226.

Khamcha, D. & Sukumal, N. 2009. *Python molurus* predation on a *Macaca nemestrina* in Khao Yai National Park, Thailand. *Hamadryad*, 34, 176-178.

Kurland, J. A. 1973. A natural history of kra macaques (*Macaca fascicularis* Raffles, 1821) at the Kutai Reserve, Kalimantan Timur, Indonesia *Primates*, 14, 245-262.

Li, D., Grueter, C. C., Ren, B., Zhou, Q., Peng, Z. & Wei, F. 2006. Characteristics of night-time sleeping places selected by golden monkeys (*Rhinopithecus bieti*) in the Samage forest, Baima Snow Mountain Nature Reserve, China. *Integrative Zoology*, 1, 141-152.

Liu, Z.-H. & Zhao, Q.-K. 2004. Sleeping sites of *Rhinopithecus bieti* at Mt. Fuhe, Yunnan. *Primates*, 45, 241-248.

Matsuda, I., Tuuga, A., Akiyama, Y. & Higashi, S. 2008. Selection of river crossing location and sleeping site by proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. *American Journal of Primatology*, 70, 1097-1101.

Matsuda, I., Tuuga, A. & Bernard, H. 2011. Riverine refuging by proboscis monkeys (*Nasalis larvatus*) and sympatric primates: Implications for adaptive benefits of the riverine habitat. *Mammalian Biology*, 76, 165-171.

Mendes Pontes, A. R. & 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.

Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. New York: John Wiley & Sons.

Oi, T. 1990. Population organization of wild pig-tailed macaques (*Macaca nemestrina nemestrina*) in West Sumatra. *Primates*, 31, 15-31.

Phoonjampa, R., Koenig, A., Borries, C., Gale, G. A. & Savini, T. 2010. Selection of Sleeping Trees in Pileated Gibbons (*Hylobates pileatus*). *American Journal of Primatology*, 71, 1-9.

Reichard, U. 1998. Sleeping sites, sleeping places, and presleep behavior of gibbons (*Hylobates lar*). *American Journal of Primatology*, 46, 35-62.

Smith, A. C., Knogge, C., Huck, M., Löttker, P., Buchanan-Smith, H. M. & Heymann, E. W. 2007. Long-term patterns of sleeping site use in wild saddleback (*Saguinus fuscicollis*) and mustached tamarins (*S. mystax*): effects of foraging, thermoregulation, predation, and resource defense constraints. *American Journal of Physical Anthropology*, 134, 340-353.

Smith, L. W., Link, A. & Cords, M. 2008. Cheek pouch use, predation risk, and feeding competition in blue monkeys (*Cercopithecus mitis stuhlmanni*). *American Journal of Physical Anthropology*, 137, 334-341.

Struhsaker, T. T. 1975. *The red colobus monkey*. Chicago: University of Chicago Press.

Sugardjito, J. 1983. Selecting nest-sites of Sumatran orangutans, *Pongo pygmaeus abelii* in the Gunung Leuser National Park, Indonesia. *Primates*, 24, 467-474.

Tenaza, R. R. & Tilson, R. L. 1985. Human predation and Kloss's gibbon (*Hylobates klossii*) sleeping trees in Siberut Island, Indonesia. *American Journal of Primatology*, 8, 299-308.

Vessey, S. H. 1973. Night observations of free-ranging rhesus monkeys. *American Journal of Physical Anthropology*, 38, 613-620.

von Hippel, F. A. 1998. Use of sleeping trees by black and white colobus monkeys (*Colobus guereza*) in the Kakamega. *American Journal of Primatology*, 45, 281-290.

Zhang, S.-Y. 1995. Sleeping habits of brown capuchin monkeys (*Cebus apella*) in French Guiana. *American Journal of Primatology*, 36, 327-335.

In the previous chapter, we showed that northern pigtailed macaques use few sleeping sites, defecate when they wake up and that all troop members sleep concentrated in a small area. Thus we think that they must create a high seed density below the sleeping trees. This may be harmful for the seed as it decreases the survival probability of many seed species. But this may be beneficial for the ecosystem as it maintain the total biodiversity (Stoner & Henry 2008) by limiting the germination of abundant seed species (through high interspecific competition within defecation site) and consequently leaving free spaces for the establishment of rarer species. Moreover, this pattern may be shown in other effective seed dispersers in the park (*e.g.* gibbons or hornbills), so as harmful for seeds it may be, it does not make pigtailed macaques less effective than others.

~~~

In the next chapter, to really understand their contribution to the ecosystem as seed dispersers, we will examine what role play macaques in a seed dispersal assemblage and what makes the service they provide necessary.
~~~

CHAPTER 5

The role of *Macaca* spp. (Primates: Cercopithecidae) in seed dispersal networks

Albert, A., Savini, T., Huynen, M.-C. The role of *Macaca* spp. (Primates: Cercopithecidae) in seed dispersal networks. Submitted to the Raffles Bulletin of Zoology.

Résumé

Pour comprendre les conséquences de l'extinction d'une espèce animale sur la survie d'une espèce végétale, il est nécessaire d'étudier les redondances fonctionnelles entre les disperseurs de graines, c'est-à-dire le chevauchement des régimes alimentaires ainsi que la redondance dans les patterns et l'efficacité de la dispersion des graines. Dans la région indo-malaise, nous observons des réseaux de disperseurs de graines incluant généralement des macaques, d'autres espèces de primates, des calaos, des bulbuls, des pigeons, des civettes et des chauves-souris. Les calaos, les gibbons et les bulbuls sont des disperseurs de graines efficaces et se complémentent dans leurs services de dispersion. Le rôle des espèces de macaques a souvent été négligé dans les études portant sur les réseaux de disperseurs, malgré leur potentielle importance dans la régénération des forêts. Cependant, beaucoup d'espèces de macaques pourraient être des disperseurs efficaces. La plupart sont frugivores et, contrairement aux autres disperseurs, peuvent manger des fruits de tous types, couleurs, tailles, contenant des graines de toutes tailles, présentant ou non une protection, et venant de plantes de toutes formes. Ils recrachent, défèquent et déposent les graines. Leur long temps de rétention intestinale, leurs longs trajets journaliers, et leurs grands domaines vitaux augmentent la probabilité qu'ils dispersent les graines aussi loin, sinon plus, que les autres frugivores. De plus, contrairement aux autres disperseurs, restreints à la canopée ou au sol, leur semi-terrestrialité leur donne accès à toutes les strates de la forêt. Finalement, plus que de simple disperseurs, les macaques peuvent jouer un rôle important dans la régénération des forêts car ils traversent tous les types de forêts, y compris les forêts dégradées, contrairement à la plupart des frugivores incapables d'utiliser les trouées dans la forêt ou les habitats ouverts. En conclusion, les macaques fournissent un complément significatif en termes de quantité dispersée et sont parfois les seuls frugivores capables de disperser les graines larges ou protégées de certaines espèces de plantes. Ils peuvent ainsi apporter à ces espèces un service de dispersion vital.

***Mots-clés* :** Macaque ; redondance fonctionnelle ; régénération de la forêt ; région indo-malaise.

Abstract

To understand the consequences of an animal extinction on the survival of a plant species, it is necessary to study the functional redundancy between seed dispersers, both diet overlap and redundancy in seed dispersal patterns and effectiveness. In the Indo-Malayan region, we observe seed dispersal networks including macaques, other primate species, hornbills, bulbuls, fruit pigeons, civets, and bats. Hornbills, gibbons, and bulbuls are effective seed dispersers and complement each other in their dispersal services. The role of *Macaca* species has been overlooked in seed dispersal network studies despite their potential importance in forest regeneration. However, many *Macaca* species could be effective seed dispersers. Most are frugivorous and, unlike other dispersers, can eat every fruit type, regardless of colour, fruit size, seed size, presence or lack of seed protection, and plant life form. They spit out, swallow, and drop seeds. Their long gut retention time, long daily travels, and large home ranges increase the probability that they disperse seeds as far as, if not farther than, other frugivores. Moreover, unlike other dispersers often restricted to canopy or ground, their semi-terrestriality gives them access to fruits of every forest strata. Finally, more than simply dispersing seeds, *Macaca* species may play an important role in forest regeneration because they cross both deforested and every forest type, unlike most other frugivores which are unable to use gaps or open habitats. In conclusion, macaques provide a significant complement in terms of dispersal quantity and are sometimes the only frugivores able to disperse the large or protected seeds of some plant species and may thus bring those species a vital dispersal service.

Key words**:** Macaque; functional redundancy; forest regeneration; Indo-Malayan region.

Introduction

Plants and animals depend on each other for their survival (Andresen 1999; Chapman & Chapman 1995). On the one hand, seed dispersal is a crucial process for plant reproduction. By moving far from the parent plant, the seeds can avoid competition and predation, and can reach suitable sites for germination and establishment (Connell 1971; Janzen 1970). On the other hand, frugivores benefit from this relation by acquiring energy through the sugar-rich flesh of fruits. By removing 70-80 % of seeds produced by canopy and sub-canopy trees, vertebrates represent the most important seed dispersal agents in Paleotropical forests (Chapman & Chapman 1999; Howe & Smallwood 1982).

The majority of fruit species are eaten by several kinds of frugivores, such as mammals and birds (Coates-Estrada & Estrada 1988; Fleming & Williams 1990; Kitamura et al. 2002; Nathan & Muller-Landau 2000). The composition of seed disperser assemblages varies according to fruit structure, size, and abundance, inducing a possible change over space and time in species which disperse a given plant species (Herrera 1985). Seed shadows (*i.e.* the spatial distribution of seeds dispersed from a single plant (Nathan & Muller-Landau 2000)) are thus determined by the combined effects of all dispersal agents (Jordano et al. 2007; Martínez et al. 2008; Nathan & Muller-Landau 2000; Spiegel & Nathan 2007). A common mistake is thinking that animals with an overlapping diet in fruit species could replace each other in terms of seed dispersal if one of them was brought to extinction. However, before concluding such a redundancy in seed dispersal services, one has to look both at overlaps in consumed species and at the seed dispersal effectiveness and patterns generated by each seed disperser for every plant species (*i.e.* functional redundancy; Brodie 2007; Clark et al. 2001; Loiselle et al. 2007; McConkey & Brockelman 2011).

Many factors influence these patterns and various animal species – characterized by their specific diets, habitat use, ranging behaviors, locomotion types, and activities – may induce various seed dispersal patterns, the sum of which may increase seed dispersal quality of a plant species (Brodie 2007; Brodie et al. 2009; Schupp et al. 2010; Spiegel & Nathan 2007).

To understand the consequences of an animal extinction on a plant species survival, it is mandatory to study the composition of frugivore assemblages at fruiting plants as well as to determine each disperser species respective role (*e.g.* Brodie et al. 2009; Lambert 1999; McConkey & Brockelman 2011; Poulsen et al. 2002; Savini & Kanwatanakid-Savini 2011) and even to understand the structure of mutualistic networks (Fortuna & Bascompte 2006). Eventually, the knowledge of the whole process is crucial for tropical forest protection because one species' disappearance could trigger cascading effects leading to the disappearance of many species – vegetal as well as animals.

In this review, we first introduce the importance of seed dispersal networks in the survival of plant populations. We then focus on how *Macaca* species, could play a crucial role in seed dispersers' assemblages using a review of the available information on *Macaca* species. Indeed this genus was often overlooked in seed dispersal network studies, whereas most findings highlight their potential importance in forest regeneration (Corlett 2009). We predicted that their eco-ethological characteristics, mainly their diet, seed processing techniques, and ranging behavior should make them as important as other dispersing frugivores usually studied in seed dispersers' assemblages.

Seed dispersal networks

Mutualistic networks

A true mutualistic interaction between two species has long been considered as existing only when both received a benefit from, and were strictly dependent on, this interaction (Stoner & Henry 2008). However, today it is increasingly accepted that mutualism may involve real networks of interacting species (Bascompte & Jordano 2006; Bascompte et al. 2003; Brodie 2007; Jordano et al. 2003) and it is frequent to observe interaction networks in which a particular plant species relies on some frugivores for seed dispersal, whereas these frugivores depend on other plant species during periods of fruit scarcity (Kaplin et al. 1998). Given these complex networks, it is difficult to predict the effects that the disappearance of one particular species could produce on the other interactants. Consequently, understanding the functioning of these networks is necessary for the establishment of adequate conservation plans, which is all the more important that the maintenance of these interactions and of the associated species is critical for the regeneration of tropical forests (Chapman 1995; Chapman & Chapman 1996; Chapman et al. 1992b; Loiselle et al. 2007). Understanding these networks' function requires the study of each participant eco-ethological characteristics, mainly focusing on their foraging behavior, which is the “main mechanism driving seed dispersal” (Jordano & Godoy 2002; p.315).

Seed size: large seeds, large dispersers

Ideally, seeds dispersed into degraded areas should include early-, mid-, and late-successional species. While growing, pioneer species, such as shrubs, quickly form a shady and humid environment essential to the survival and growth of mid- and late-successional species. However, Duncan and Chapman (1999) showed that 99.9% of seeds recovered in a deforested agricultural area were early-successional species already present and fruiting on the site. This seems logical since these species often produce larger numbers of seeds compared with mid- and late-successional species. Hence, the most important role of frugivores appears: the seed dispersal of mid- and late-successional species, mainly large-seeded species characteristic of the ultimate stage of succession (Kaplin & Moermond 1998; Parrotta et al. 1997). Large-seeded species are better competitors than small-seeded species as they have better survival probabilities and are more competent in establishment (Murali 1997). But these advantages cannot counteract the fact that they are poorer colonizers (Dominy & Duncan 2005) as their dispersal can only be realized by a few groups of large frugivores (Corlett 1998; Kitamura et al. 2002), such as large birds and mammals. Indeed, the maximum size of seeds dispersed by any animal species depends on the size of its mouth (Forest Restoration Research Unit 2006) and so on the size of its body. Consequently the number of frugivore species that serves a given plant species declines with seed size (Chapman et al. 1992a; Kitamura et al. 2002; Peres & van Roosmalen 2002). Large-seeded species are thus more threatened than others as they depend on a restricted number of seed dispersers thought to be vulnerable to extinction, due to selective hunting (Chapman et al. 2009; Kitamura et al. 2002) and to habitat loss or degradation (Corlett 1998; Kitamura et al. 2002; Melo et al. 2010). The disappearance of their dispersers could bring large-seeded species to extinction because of the low probability of finding seed dispersers with a similar role.

Many studies highlight the role of birds and bats in seed dispersal (Fleming & Heithaus 1981; Herrera 1984; Medellin & Gaona 1999) but other targeted primates as essential within dispersers’ assemblages (Dew & Wright 1998; Garber & Lambert 1998; Lambert & Chapman 2005; Poulsen et al. 2001; Wrangham et al. 1994). Specifically, primates are particularly apt at dispersing large-seeded or hard-husked fruit species, which may be inaccessible to smaller taxa, or may be hard to process (Chapman & Russo 2007; Kaplin & Lambert 2002).

Macaques: overlooked associates

Tropical forests of the Indo-Malayan region share many of the same families and genera of animals (Corlett 1998). Thus, it is common to observe networks of potentially effective seed dispersers, including macaques – one or several species –, some other primate species – mainly arboreal ones (*e.g.* langurs, gibbons) –, hornbills, bulbuls, fruit pigeons, civets, and bats (Boon & Corlett 1989; Borries et al. 2002; Corlett 1998; Ganesh & Davidar 2005; Lucas & Corlett 1998; McConkey & Brockelman 2011; Savini & Kanwatanakid-Savini 2011; Srivastava 2006). Other frugivores, such as elephants, deers, bovids, tapirs, and bears may complete the network, depending on the area. Two *Macaca* species are exceptions according to the habitat and climate where they live. *M. fuscata* lives in Japanese temperate forests where the climate varies with altitude from sub-tropical, warm temperate to cool temperate, tending to sub-alpine. *M. fuscata* is thus part of a different seed dispersal network only made by birds (mainly thrushes, pigeons and bulbuls (Noma & Yumoto 1997)), and deers (*Cervus nippon yakushimae*). *M. sylvanus*, the only species outside Tropical Asia, lives in the Atlas Mountains of Algeria and Morocco with a small population of unknown origin in Gibraltar. It is also the only macaque species to be highly herbivorous and granivorous and its role as seed disperser could thus be negligible. Another species, *Macaca thibetana*, has much of its range outside the Indo-Malayan region and may be found in tropical, subtropical as well as temperate forests.

Some disperser species' networks have been better studied than others. Seed dispersal by hornbills (Kitamura et al. 2006; Kitamura et al. 2004a; Kitamura et al. 2002), gibbons (Brodie et al. 2009; Kitamura et al. 2002; Whitington 1990) and bulbuls (Khamcha 2009; Kitamura et al. 2002), and the network interaction between several of them (McConkey & Brockelman 2011; Savini & Kanwatanakid-Savini 2011) have been well studied and we know that beyond being simply effective seed dispersers alone (Corlett 2002), these taxa may also complement each other in their dispersal services (McConkey & Brockelman 2011; Savini & Kanwatanakid-Savini 2011). Gibbons seem to be prevalent as they disperse a medium number of seeds belonging to many plant species, including fruit with hard covers and flesh attached to seeds that hornbills are unable to eat (Kanwatanakid 2000; Kitamura et al. 2004b). However, due to their small home ranges (Table 5.1), gibbons disperse seeds over a small area (Savini & Kanwatanakid-Savini 2011). Hornbills are less frugivorous (Kanwatanakid-Savini et al. 2009) and disperse less seed species, but over a larger area during non-breeding seasons, and are able to consume dehiscent fruits usually ignored by gibbons (Savini & Kanwatanakid-Savini 2011). Bulbuls seem to be similar to gibbon in that they disperse many seed species over small areas (Khamcha 2009). However, they have a very short gut retention time which decreases the probability of harmful scarification of the ingested seeds and they forage in the lower to middle strata of the canopy (Khamcha 2009). Moreover, contrary to gibbons and large hornbills, they only disperse small-seeded species (Khamcha 2009).

Other species could be essential parts of the seed dispersal assemblage found in the Indo-Malayan region. Some herbivores have been shown to provide effective dispersal services to plant species with particular requirements. For instance, munjacs (*Muntiacus muntjak*) are the most effective dispersers for *Choerospondias axillaris* (Anacardiaceae) seeds in Khao Yai National Park, Thailand (Brodie et al. 2009; Chanthorn & Brockelman 2008), although deers seem to be mostly seed predators (Corlett 1998). Indian rhinoceros (*Rhinoceros unicornis*) may be the major dispersal agent for *Trewia nudiflora* (Euphorbiaceae) seeds, in Chitwan, lowland Nepal (Corlett 1998). Elephants (*Elephas maximus*) could also play a vital role for some plant species, like their African relatives, *Loxodonta africana* (Babweteera et al. 2007; Chapman et al. 1992b). But these species still need to be studied as seed dispersers, along with sambars (*Cervus unicolor*), or gaurs (*Bos gaurus*). Even some frugivore species have long been overlooked in seed dispersal network studies, such as bats, due to their nocturnal habits, or macaques, although *Macaca* is one of the most widespread genera of non-human primates.

Thus, data are lacking and studies on macaque seed dispersal habits come mainly from the Khao Yai National Park (Thailand; *M. leonina*), the Yakushima island (Japan*; M. fuscata*), Singapore (*M. fascicularis*) and Hong Kong (*M. fascicularis*, *M. mulatta*), with some other rare studies from Malaysia (*M. fascicularis*), Taiwan (*M. cyclopis*), and Western Ghats (India*; M. silenus*). However, given their diet, seed processing techniques, and ranging behavior, many *Macaca* species could be effective seed dispersers (Corlett 2002; McConkey & Brockelman 2011).

Table 5.1. Characteristics of various dispersal agents found in the Indo-Malayan region.

	Gibbons (14 spp.)	**Hornbills (small/large)**	**Bulbuls**	**Pigeons**	**Civets (11 spp.)**	**Deers (15 spp.)**	**Bears (3 spp.)**	**Elephants (1 sp.)**
No fruit species	84 [b]	71 [b]	118 [b]	62 [b]	56 [b]	46 [b]	13 [b]	9 [b]
Fruit colour	Red, black, yellow-orange [a, b]	Red, black, purple [a, b]	Red, purple, black [b]	Red, purple, black [b]	Red, black, yellow [b]	Red, black, yellow [b]	Red, purple, black, yellow [b]	Yellow [b]
Seed processing	Swallow	Spit out (swallow very small seeds)	Swallow	swallow	swallow	swallow	swallow	swallow
Seed dispersed/Total ingested	90% [a]	100% [a]	-	-	-	-	-	75% [g]
Maximum diameter of ingested seed (mm)	19 [b]	Spit out: 35 Swallow: 0,05 [a]	13 [b]	20 [b]	17 [b]	28 [b]	13 [b]	23 [b]
Seed passage time (min)	900-3000 [p]	Sallow: 83 (up to 600) Spit out: 67 [a]	5-122 [k]	20-530 [q]	156 [i]	-	186-2640 [j]	558-6828 [g]

Seed dispersal distance (m)	100-1000 [d]	1000-10,000 [d]	Up to 454 [c]	>10,000 [d]	1000-10,000 [d]	1000-10,000 [d]	Up to 22,000 [j]	Up to 5772 [g]
Deposition pattern	Clumped Scattered	Scattered	Scattered	Scattered	Clumped	Clumped	Clumped	Clumped
Germination percentage	95.5% [a]	95.8% [a]	-	-	-	-	44-63% [n]	60% [e]
Dispersal of arboreal shrubs	No [b]	No [b]	Yes [b]	-	-	-	-	No [b]
Biomass (kg/km^2)	105 [a]	38.7 [a]	11.1 [c]	-	-	14-117 [f]	5-15 [o]	-
Home range size (ha)	25 [a]	100 (small) 800-4200 (large) [a]	2.2 [c]	-	300-1700 [l]	-	1000-18,000 [m]	5000-100,000 ha [h]
Travel (m/day)	1300 [a]	4500 (small) 8500-11,000 (large) [a]	-	-	-	-	-	1000-2000 [g]
Foraged canopy strata	Outer to emergent [a]	Emergent (large) Middle (small) [a]	Lower to middle [c]	-	-	Ground [b]	-	Ground [b]
Forest type	Primary [a]	Primary Secondary [a]	Primary Secondary [k]	-	-	Primary Secondary	Primary Secondary	Primary Secondary

Seed accumulation	Sleeping sites Fruiting trees Travel pathways	Nesting sites (breeding season) Roosting sites (non-breeding season) Travel pathways	Nesting sites Roosting sites	-	-	-	-	Travel pathways

---

[a] (Savini & Kanwatanakid-Savini 2011), [b] (Kitamura et al. 2002), [c] (Khamcha, unpublished data), [d] (Corlett 2009), [e] (Kitamura et al. 2007), [f] (Brodie et al. 2009), [g] (Campos-Arceiz et al. 2008), [h] (Sukumar 2006), [i] (Nakashima & Sukor 2009), [j] (Koike et al. 2011), [k] (Weir & Corlett 2007), [l] (Rabinowitz 1991), [m] (Kozakai et al. 2011); [n] (Koike et al. 2008); [o] (Ngoprasert et al. in revision); [p] (McConkey 2000); [q] (Corlett 1998)

Macaques in Asian seed dispersal networks

Diet

Macaques are omnivorous-frugivorous primates, *i.e.* they eat fruits, but also leaves, flowers, shoots, roots, invertebrates, and small animals in variable quantities (Caldecott 1986; Krishnamani 1994; Kurup & Kumar 1993; Maruhashi 1980; O'Brien & Kinnaird 1997; Rowe & Myers 2011; Schülke et al. 2011; Su & Lee 2001). The percentage of fruit in the diet, usually higher than other food items, depends on the particular macaque species – from relatively low (10-32% in *M. fuscata*; Agetsuma & Nakagawa 1998) to very high (85% in *M. nigrescens*; Rowe & Myers 2011) – but may also show intra-specific variations, depending on habitat and provisioning (*e.g.* in *M. fuscata*: 15% in provisioned troops (Son 2003) and 88% in unprovisioned ones (Wheatley 1980)), and seasonal variations (Hanya et al. 2003) (Table 5.2). The number of fruit species included in the macaques' diet is species-specific but often higher than for other sympatric frugivores (Table 5.1 and 5.2) (Corlett 1998).

Fruit species are not restricted to the so-called 'primate fruits', those with large seeds, orange-brown color, and a protective rind (Corlett 1998) as macaques eat various fruit types, included dehiscent and indehiscent fruits – contrary to other mammals tending to avoid dehiscent fruits, preferred by birds (Kitamura et al. 2002; Lucas & Corlett 1998) –, protected or not – contrary to other frugivores preferring unprotected fruits (Corlett 1998)– of every color – when other mammals prefer yellow fruits (Kitamura et al. 2002).

The few number of studies focused on macaque seed dispersal seem to show that they may disperse very small (*e.g. M. fascicularis*: 0.2 mm; Lucas & Corlett 1998), as well as very large seeds (*e.g. M. cyclopis*: up to 16.7 mm for swallowed seeds (Chen 1999); *M. fascicularis*: up to 30 mm for spat out seeds and 51.3 mm for dropped seeds (Lucas & Corlett 1998); *M. fuscata*: up to 26 mm for swallowed seeds and 40 mm for spat out seeds (Otani 2004)), such as deers, but contrary to other frugivores which are more restricted to some seed sizes (*e.g.* small seeds for most birds and bats and large seeds for elephants) (Kitamura et al. 2002; Lucas & Corlett 1998).

Moreover, they feed on small as well as very large fruits (*e.g.* 2.4 to 84.3 mm in *M. leonina*; Kitamura et al. 2002), the latter excluding seed dispersal by all birds but hornbills and fruit pigeons (Corlett 1998). Thus, in some areas where macaques are the only large frugivores, they may be essential for the dispersal of medium- and large-sized fruits (*e.g. M. fuscata* on Yakushima island (Noma & Yumoto 1997), and *M. fascicularis* in Singapore and

Hong Kong (Corlett 1996; Lucas & Corlett 1998)). In Khao Yai National Park, several large-seeded plant species, such as *Platymitra macrocarpa*, *Nephelium melliferum*, *Baccaurea ramiflora*, *Lansium domesticum* (Kitamura et al. 2005) and *Prunus javanica* (McConkey & Brockelman 2011) have been shown to be mainly dispersed by primates (*Macaca leonina* and *Hylobates lar*). On Yakushima island, *M. fuscata* could be, along with resident fruit pigeons, an essential seed disperser for large-fruited plant species and species fructifying in summer, such as *Myrica rubra* (Myricaceae). Indeed, they are resident on the island and feed on fruits all-year long contrary to most bird species only present in winter (Noma & Yumoto 1997).

Finally, macaques eat fruits produced by all plant life forms (*i.e.* tall and small trees, lianas, shrubs, and herbs; Caldecott 1986; Chen 1999; Kitamura et al. 2002; Kumar et al. 2007; Lindburg 1977; Ramachandran & Joseph 2000) while other frugivores usually ignore small trees and shrubs, necessary for forest succession, and deers and elephants only eat the fallen fruits of tall trees (Kitamura et al. 2002).

Table 5.2. Characteristics of *Macaca* species.

***Macaca* species**	**Common name**	**Home range (ha)**	**Daily range (m/d)**	**No fruit species**	**% fruit in diet**
M. arctoides	Stump-tailed	-	-	-	-
M. assamensis	Assamese	95-500[a]	1900[a]	-	42.2%[v]
M. cyclopis	Formosan rock	130[a]	2065[a]	51[k]-66[j]	52%[w]
M. fascicularis	Long-tailed	7-300[a]	1900[b]	185[l]	15% (Provisioned)[x] 88.31%[y]
M. fuscata	Japanese	214-797[a]	1218[a]	45[m, n]	10.2-31.6%[z]
M. hecki	Heck's	-	-	-	
M. leonina	Northern pigtailed	83-347[a]	690-2240[a]	126[o]	41% (Semi-provisioned)[o] 65.9%[aa]
M. maura	Moor	20[a]	-		
M. mulatta	Rhesus	130-1340[c]	1050-3500[c]	28[p]	65-70%[p]
M. munzala	Arunachal	11-28[h]	1500[h]	11[h]	68%[h]

M. nemestrina	Southern pigtailed	62-828[d]	902-2960[d]	146[q]	74.2%[q]
M. nigra	Celebes crested	175-341[a]	1750-3140[a]	145[r]	60-70.7%[r]
M. nigrescens	Gorontalo	-	515-1240[a]	-	85.1%[a]
M. ochreata	Booted	29-85[g]	-	-	66%[bb]
M. pagensis	Pagai Island	-	-	-	
M. radiata	Bonnet	2-500[a]	710-1300[a]	16[s]	47.9%[s]
M. siberu	Siberut	530[a]	-	-	50%[a]
M. silenus	Lion-tailed	131[e]	750-2500[e]	33[t]	61.9%[a]
M. sinica	Toque	41[a]	500-2000[a]	-	66%[a]
M. sylvanus	Barbary	200-720[a]	2000-9000[a]	-	33%[a]
M. thibetana	Milne-edwards'	500[a]	-	-	-
M. tonkeana	Tonkean	67-143[f]	707-1500[i]	58[u]	66.8-79.8%[u]

[a] (Rowe & Myers 2011); [b] (Wheatley 1980); [c] (Makwana 1978); [d] (Caldecott 1986); [e] (Kurup & Kumar 1993); [f] (Riley 2007); [g] (Astaras & Waltert 2010); [h] (Kumar et al. 2007); [i] (Pombo et al. 2004); [j] (Chen 1999); [k] (Su & Lee 2001); [l] (Lucas & Corlett 1998); [m] (Hanya 2004); [n] (Maruhashi 1980); [o] (Albert, unpublished data); [p] (Lindburg 1977); [q] (Caldecott 1986); [r] (O'Brien & Kinnaird 1997); [s] (Krishnamani 1994); [t] (Umapathy & Kumar 2000); [u] (Riley 2007); [v] (Schülke et al. 2011); [w] (Chang 1999); [x] (Son 2003); [y] (Wheatley 1980); [z] (Agetsuma & Nakagawa 1998); [aa] (Choudhury 2008); [bb] (Priston 2005)

Seed processing

Seeds may be swallowed, spat out, or dropped (Chen 1999; Kitamura et al. 2002; Lucas & Corlett 1998) depending on seed species. When swallowed, they are retained for a long duration in the gut as, like most cercopithecines, macaques have a long gut retention time. In *Macaca fuscata yakui*, Otani (2004) estimated an average retention time of 39.1 ± 3.3 h for the consumption of *Eurya emarginata* seeds, and Tsuji (2010) estimated an average retention time reaching 54 h. In *Macaca cyclopis*, Chen (1999) recorded an average retention time of 36.4 ± 5.4 h. This is significantly higher than most other dispersers (Khamcha 2009; Kitamura 2007; Savini & Kanwatanakid-Savini 2011), but comparable to gibbons (15-50 h; McConkey 2000; Savini & Kanwatanakid-Savini 2011), bears (3.1-44 h; Koike et al. 2011), or even elephants (9.3-113.8 h; Kitamura et al. 2007) (Table 5.1). Thus, they may potentially disperse seeds far from the parent plant. Moreover, if a long retention time is often considered as potentially harmful for ingested seeds, many studies have shown that gut treatment by primates was mostly neutral (Traveset 1998) and this seems to be the case for macaque species (Chen 1999; McConkey & Brockelman 2011; Chapter 2).

Macaques defecate individually, contrary to gibbons, but mainly from low branches or on the ground where they spend the largest amount of their day time (Table 5.2). Thus, their cohesive dungs are unlikely to be broken up during the fall, leaving seeds highly clumped by sometimes up to several hundreds (Lucas & Corlett 1998; Otani 2004), contrary to birds, bats, and arboreal primate feces, which usually shatter before reaching the ground (Boon & Corlett 1989; Corlett 1998). This clumped deposition may have harmful consequences for seeds prone to density-dependent pathogens or predators (Howe 1989). However, *M. silenus*, and *M. sinica* are exceptions which, due to their arboreal habits, may defecate from higher heights and increase the probability that feces will scatter by falling through vegetation.

Macaques, due to their cheek pouches, may spit out seeds. In every macaque species, the cheek pouches are highly developed (Murray 1975). This can be due to their extensive use, during which monkeys store large amounts of fruits and seeds and, thus, increase the probability of seed dispersal. Although they spit out many seeds under the parent trees (McConkey & Brockelman 2011) – a behavior also seen in other dispersers such as flying foxes (Corlett & Lucas 1989) – a significant percentage of seeds are spat out beyond the crown edge (McConkey & Brockelman 2011). Macaques also drop seeds but this technique seems to be mainly used for very large-seeded fruits (Lucas & Corlett 1998; Chapter 2).

Thanks to these various processing techniques, macaques are able to disperse seeds up to several hundred meters (Huang 2005; Tsujino & Yumoto 2009; Chapter 2), much like gibbons (Corlett 2009), and sometimes up to 2.4 km (Chen 1999), a distance comparable to dispersal by hornbills, bulbuls and civets (Corlett 2009; Khamcha, unpublished data).

For a long time, macaques were considered as seed predators. However, the proportion of seed species destroyed by macaques seems to be low given seed destruction is encountered mainly in two cases: predation on seeds of Fagaceae and feeding on immature fruits (Corlett 1998; Hanya 2005; Lindburg 1977; Lucas & Corlett 1998; Maruhashi 1980; O'Brien & Kinnaird 1997; Otani 2004).

Ranging behavior

Macaques are all semi-terrestrial, with *M. silenus* and *M. sinica* being arboreal. This enables them to survive in poor forests with scarce and scattered food sources. Terrestrial travels between arboreal food sources are rapid and energy efficient (Rodman 1979). This traveling mode enables them to use an increased diversity of food sources including fallen fruits (Caldecott et al. 1996) to which arboreal species do not have access. Macaques thus have the possibility to forage in all strata of the forest canopy whereas other frugivores are either canopy dwellers or terrestrial animals that only eat fallen fruits (Kitamura et al. 2002). This is probably why most macaques are able to live in primary and secondary forests.

Macaques, while foraging, continuously progress across the smaller home ranges of other species included in their own home range (*e.g.* langurs). They quickly harvest the highest quality foods as they pass on to other food patches (Caldecott 1986). The fast terrestrial travels of macaques, along with a long daily range (from 500 to 3140 m/day; Rowe & Myers 2011), induce usually large home ranges (from 20 to 1340 ha; Rowe & Myers 2011), increasing the probability that seeds will be dispersed far from the parent tree, and often farther than where seeds would be dispersed by most frugivorous birds (except hornbills), which have small home ranges (Hanya 2005).

Finally, macaques are tolerant to human disturbance, and may cross disturbed areas, even urbanized areas for some species (Kumar et al. 2007; Lucas & Corlett 1998; Makwana 1978; Maruhashi 1980; O'Brien & Kinnaird 1997; Riley 2007; Sinha 2001). Their seed dispersal role may be essential to the regeneration of secondary forests in these areas (Corlett 1998; Lucas & Corlett 1998) as few frugivores may survive in disturbed forests, except bulbuls (Corlett 1998) which disperse only small seeds.

Conclusion

Several frugivore species known to be effective seed dispersers coexist with macaques. However, macaques could be equally able as seed dispersers. They eat fruits in quantity, which implies the potential dispersal of many seeds. Thus, they may defecate as many, or even more, seeds than gibbons (McConkey & Brockelman 2011), for example, which are considered to be very good seed dispersers in forests of the Indo-Malayan region. Macaques eat a high number of species, more than other frugivores, which may increase the dilution of seeds carried out during digestion. Indeed, if a greater number of species is consumed, a more restricted number of seeds of the same species is found in the same dung. Thus, clumping is less important and the dispersal of better quality. Like gibbons (McConkey 2000), their gut seems to process seeds with care. They have cheek pouches, which enable them to store and transport seeds away from the parent tree before spitting out the seeds. They have large home ranges, larger than some other primate species considered to be good seed dispersers, such as gibbons (Savini 2005). But, more than simply dispersing seeds, some *Macaca* species may play an important role in various succession stages during forest regeneration given they cross a range of forest types within the same day (primary and secondary forests), and even deforested areas, contrary to gibbons unable to use gaps or open habitats. They move fast on the ground, which increases dispersal distances. They eat fruits of plant species belonging to all plant life forms present in the forest. According to Kitamura *et al.* (2002), pigtailed macaques and bulbuls are the only seed dispersers consuming the fruits of arboreal shrubs in KYNP. However these shrubs play a central role at the beginning of succession because they enable the future establishment of sun-intolerant species, particularly with a supply of shade and moisture on the floor. Moreover, they belong to the rare large frugivores still present in the Indo-Malayan region, and are potentially able to disperse large seeds. However, many primary forest species are characterized by their large seeds. After enabling shrub establishment, macaques are part of the only frugivorous species able to bring seeds of primary forest trees. In the same way, macaques could be vital dispersers for some pioneer species remaining as mature plants in primary forests. Their seedlings might not survive in close forests, and would need to be dispersed in open areas that few disperser species can cross.

In conclusion, we believe *Macaca* species are important associates in the seed dispersal assemblage found in forests of the Indo-Malayan region because they may disperse most plant species usually more efficiently dispersed by birds, bats, gibbons, or civets (Corlett 1998; Kitamura et al. 2002; Kitamura et al. 2005), and, thus, provide a significant complement in terms of dispersal quantity. Moreover, within assemblages of dispersing frugivores, they are sometimes the only one able to disperse seeds of some species, mainly large-seeded or protected species (Corlett 1998), and may thus bring them a vital dispersal service. Macaques could be the last, but not least element of a necessary seed dispersal network.

This kind of network between a primate and other frugivores is not unique to Asia as we can observe similar networks in Africa and South America. Indeed, African frugivore networks often include cercopithecine species (mainly *Cercopithecus* spp., but also *Papio* spp. and *Lophocebus* spp.), other primate species (mainly chimpanzees), hornbills, fruit pigeons, bulbuls, sturnids, and bats (Forget et al. 2007; Kirika et al. 2008; Lambert 2010;

Poulsen et al. 2002). In South America, cercopithecines are absent but other primate species (*Ateles* spp., *Alouatta* spp. and *Saguinus* spp.) take part of networks including also thrushes, toucans, deers, and bats (Culot 2009; Howe 1983; Nuñez-Iturri & Howe 2007; Russo 2003; Terborgh et al. 2008). These species seem to complement each other in seed dispersal service in the same way as in Asian frugivore networks.

Acknowledgments

We thank Richard Corlett for his valuable comments on a previous draft of this review and Lee Olsen for editing the English.

Literature cited

Agetsuma, N. & Nakagawa, N. 1998. Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. *Primates*, 39, 275-289.

Andresen, E. 1999. Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. *Biotropica*, 31, 145-158.

Astaras, C. & Waltert, M. 2010. What does seed handling by the drill tell us about the ecological services of terrestrial cercopithecines in African forests? *Animal Conservation*, 13, 568-578.

Babweteera, F., Savill, P. & Brown, N. 2007. *Balanites wilsoniana*: Regeneration with and without elephants. *Biological Conservation*, 134, 40-47.

Bascompte, J. & Jordano, P. 2006. The structure of plant-animal mutualistic networks. In: *Ecological networks* (Ed. by Pascual, M. & Dunne, J.), pp. 143-159. Oxford, US: Oxford University Press.

Bascompte, J., Jordano, P., Melián, C. J. & Olesen, J. M. 2003. The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100, 9383-9387.

Boon, P. P. & Corlett, R. 1989. Seed dispersal by the lesser short-nosed fruit bat (*Cynopterus brachyotis*, Pteropodidae, Megachiroptera). *Malayan Nature Journal*, 42, 251-256.

Borries, C., Larney, E., Kreetiyutanont, K. & Koenig, A. 2002. The diurnal primate community in a dry evergreen forest in Phu Khieo wildlife sanctuary, Northeast Thailand. *Natural History Bulletin of the Siam Society*, 50, 75-88.

Brodie, J. F. 2007. Effects of seed dispersal by gibbons, sambar, and muntjac on *Choerospondias axillaris* demography, and the disruption of this mutualism by wildlife poaching. PhD, University of Montana.

Brodie, J. F., Helmy, O. E., Brockelman, W. Y. & Maron, J. L. 2009. Functional differences within a guild of tropical mammalian frugivores. *Ecology*, 90, 688-698.

Caldecott, J. O. 1986. *An ecological and behavioural study of the pig-tailed macaque*. Basel: Karger.

Caldecott, J. O., Feistner, A. T. C. & Gadsby, E. L. 1996. A comparison of ecological strategies of pig-tailed macaques, mandrills and drills. In: *Evolution and ecology of macaque societies* (Ed. by Fa, J. E. & Lindburg, D. G.), pp. 73-94. Cambridge Cambridge University Press.

Campos-Arceiz, A., Larrinaga, A. R., Weerasinghe, U. R., Takatsuki, S., Pastorini, J., Leimgruber, P., Fernando, P. & Santamaría, A. L. 2008. Behavior rather than diet mediates seasonal differences in seed dispersal by Asian elephants. *Ecology*, 89, 2684-2691.

Chang, K. 1999. Foraging strategies of Formosan macaques (*Macaca cyclopis*) in Fushan Experimental Forest. Dissertation, National Taiwan University.

Chanthorn, W. & Brockelman, W. Y. 2008. Seed dispersal and seedling recruitment in the light-demanding tree *Choerospondias axillaris* in old-growth forest in Thailand. *ScienceAsia*, 34, 129-135.

Chapman, C. A. 1995. Primate seed dispersal: Coevolution and conservation implications. *Evolutionary Anthropology*, 4, 74-82.

Chapman, C. A. & Chapman, L. J. 1995. Survival without dispersers: seeding recruitment under parents. *Conservation Biology*, 9, 675-678.

Chapman, C. A. & Chapman, L. J. 1996. Frugivory and the fate of dispersed and nondispersed seeds in six African tree species. *Journal of Tropical Ecology*, 12, 491-504.

Chapman, C. A. & Chapman, L. J. 1999. Forest restoration in abandoned agricultural land: A case study from East Africa. *Conservation Biology*, 13, 1301-1311.

Chapman, C. A., Chapman, L. J., Wrangham, R., Hunt, K., Gebo, D. & Gardner, L. 1992a. Estimators of fruit abundance of tropical trees. *Biotropica*, 24, 527-531.

Chapman, C. A. & Russo, S. E. 2007. Primate seed dispersal: Linking behavioral ecology with forest community structure. In: *Primates in perspective* (Ed. by Campbell, C. J., Fuentes, A. F., MacKinnon, K. C., Panger, M. & Bearder, S.), pp. 510-525. Oxford: Oxford University Press.

Chapman, H. M., Goldson, S. L. & Beck, J. 2009. Postdispersal removal and germination of seed dispersed by *Cercopithecus nictitans* in a West African montane forest. *Folia primatologica*, 81, 41-50.

Chapman, L. J., Chapman, C. A. & Wrangham, R. 1992b. *Balanites wilsoniana*: elephant dependent dispersal? *Journal of Tropical Ecology*, 8, 275-283.

Chen, C. E. 1999. The influence of Formosan macaques (*Macaca cyclopis*) on seed dispersal in Fushan experimental forest M.S. thesis, National Taiwan University.

Choudhury, A. 2008. Ecology and behaviour of the Pig-tailed macaque *Macaca nemestrina leonina* in some forests of Assam in north-east India. . *Journal of the Bombay Natural History Society*, 105, 279-291.

Clark, C. J., Poulsen, J. R. & Parker, V. T. 2001. The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. *Biotropica*, 33, 606-620.

Coates-Estrada, R. & Estrada, A. 1988. Frugivory and seed dispersal in *Cymbopetalum baillonii* at Los Tuxtlas, Mexico. *Journal of Tropical Ecology*, 4, 157-172.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of populations* (Ed. by den Boer, P. J. & Gradwell, G. R.), pp. 298-312. Wageningen, The Netherlands: Centre for Agricultural Publication and Documentation.

Corlett, R. T. 1996. Characteristics of vertebrate-dispersed fruits in Hong Kong. *Journal of Tropical Ecology*, 12, 819-833.

Corlett, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews*, 73, 413-448.

Corlett, R. T. 2002. Frugivory and seed dispersal in degraded tropical East Asian landscape. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 451-465. New York: CABI Publishing.

Corlett, R. T. 2009. Seed dispersal distances and plant migration potential in tropical East Asia. *Biotropica*, 41, 592-598.

Corlett, R. T. & Lucas, P. W. 1989. Consumption of *Campnospermum auriculatum* (Anacardiaceae) fruit by vertebrates in Singapore. *Malayan Nature journal*, 42, 273-276.

Culot, L. 2009. Primary seed dispersal by two sympatric species of tamarins, *Saguinus fuscicollis* and *Saguinus mystax*, and post-dispersal seed fate. PhD thesis, Université de Liège.

Dew, J. L. & Wright, P. 1998. Frugivory and seed dispersal by four species of primates in Madagascar's Eastern rain forest. *Biotropica*, 30, 425-437.

Dominy, N. J. & Duncan, B. W. 2005. Seed-spitting primates and the conservation and dispersion of large-seeded trees. *International Journal of Primatology*, 26, 631-649.

Duncan, R. S. & Chapman, C. A. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications*, 9, 998-1008.

Fleming, T. H. & Heithaus, E. R. 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica*, 13, 45-53.

Fleming, T. H. & Williams, C. F. 1990. Phenology, seed dispersal, and recruitment in *Cecropia peltata* (Moraceae) in Costa Rican tropical dry forest. *Journal of Tropical Ecology*, 6, 163-178.

Forest Restoration Research Unit. 2006. *How to plant a forest: the principles and practice of restoring tropical forests*. Biology Department, Science Faculty, Chiang Mai University, Thailand.

Forget, P.-M., Dennis, A. J., Mazer, S. J., Jansen, P. A., Kitamura, S., Lambert, J. E. & Westcott, D. A. 2007. Seed allometry and disperser assemblages in tropical rainforests: a comparision of four floras on different continents. In: *Seed dispersal: theory and its application in a changing world* (Ed. by Dennis, A. J., Schupp, E. W., Green, R. J. & Westcott, D.), pp. 5-36. Wallingford, UK: CAB International Publishing.

Fortuna, M. A. & Bascompte, J. 2006. Habitat loss and the structure of plant-animal mutualistic networks. *Ecology Letters*, 9, 281-286.

Ganesh, T. & Davidar, P. 2005. Fruiting phenology and pre-dispersal seed predation in a rainforest in southern western Ghats, India. In: *Tropical fruits and frugivores: The search of strong interactors* (Ed. by Dew, J. L. & Boubli, J.-P.), pp. 139-154. Dordrecht: Springer.

Garber, P. A. & Lambert, J. E. 1998. Introduction to primate seed dispersal. Primates as seed dispersers: ecological processes and directions for future research. *American Journal of Primatology*, 45, 3-8.

Hanya, G. 2004. Diet of a Japanese macaque troop in the coniferous forest of Yakushima. *International Journal of Primatology*, 25, 55-71.

Hanya, G. 2005. Comparisons of dispersal success between the species fruiting prior to and those at the peak of migrant frugivore abundance. *Plant Ecology*, 181, 167-177.

Hanya, G., Noma, N. & Agetsuma, N. 2003. Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima. *Primates*, 44, 51-59.

Herrera, C. M. 1984. A study of avian frugivores, bird-dispersed plants, and their interaction in mediterranean scrublands. *Ecological Monographs*, 54, 1-23.

Herrera, C. M. 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos*, 44, 132-141.

Howe, H. F. 1983. Annual variation in a neotropical seed-dispersal system. In: *Tropical rain forest: ecology and management* (Ed. by Sutton, S. L., Whitmore, T. C. & Chadwick, A. C.), pp. 211-227. Oxford: Blackwell Scientific Publications.

Howe, H. F. 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia*, 79, 417-426.

Howe, H. F. & Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13, 201-228.

Huang, C.-L. 2005. Effects of dispersal via cheek pouches of Formosan macaques (*Macaca cyclopis*) on seed shadow and seed fate of three Lauraceae species at Fushan experimental forest, National Taiwan University.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist*, 104, 501-528.

Jordano, P., Bascompte, J. & Olesen, J. M. 2003. Invariant properties in coevolutionary networks of plant-animal interactions. *Ecology Letters*, 6, 69-81.

Jordano, P., García, C., Godoy, J. A. & García-Castaño, J. L. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 3278-3282.

Jordano, P. & Godoy, J. A. 2002. Frugivore-generated seed shadows: a landscape view of demographic and genetic effects. In: *Seed-dispersal and frugivory: ecology, evolution* *and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 305-321. New York: CAB International.

Kanwatanakid, C.-O. 2000. Characteristics of fruits consumed by the white-handed gibbon (*Hylobates lar*) in Khao Yai National Park, Thailand. PhD thesis, Mahidol University.

Kanwatanakid-Savini, C.-O., Poonswad, P. & Savini, T. 2009. An assessment of food overlap between gibbons and hornbills. *The Raffles Bulletin of Zoology*, 57, 189-198.

Kaplin, B. A. & Lambert, J. E. 2002. Effectiveness of seed dispersal by *Cercopithecus* Monkeys: Implications for seed input into degraded areas. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 351-364. New York: CABI Publishing.

Kaplin, B. A. & Moermond, T. C. 1998. Variation in seed handling by two species of forest monkeys in Rwanda. *American Journal of Primatology*, 45, 83-101.

Kaplin, B. A., Munyaligoga, V. & Moermond, T. C. 1998. The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*). *Biotropica*, 30, 56-71.

Khamcha, D. 2009. Movement patterns, seed dispersal and tree-fall gap use by a forest interior frugivore: puff-throated bulbul (*Alophoixus pallidus*). Master thesis, King Mongkut’s University of Technology Thonburi.

Kirika, J. M., Bleher, B., Böhning-Gaese, K., Chira, R. & Farwig, N. 2008. Fragmentation and local disturbance of forests reduce frugivore diversity and fruit removal in *Ficus thonningii* trees. *Basic and Applied Ecology*, 9, 663-672.

Kitamura, S. 2007. Current knowledge and future issues for frugivory and seed dispersal by animals in Southeast Asia: special reference to large frugivorous birds and mammals. *Japanese Journal of Ecology*, 57, 159-171.

Kitamura, S., Suzuki, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T., Noma, N. & Suckasam, C. 2006. Dispersal of *Canarium euphyllum* (Burseraceae), a large-seeded tree species, in a moist evergreen forest in Thailand. *Journal of Tropical Ecology*, 22, 137-146.

Kitamura, S., Suzuki, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Noma, N., Maruhashi, T. & Suckasam, C. 2004a. Dispersal of *Aglaia spectabilis*, a large-seeded tree species in a moist evergreen forest in Thailand. *Journal of Tropical Ecology*, 20, 421-427.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P. & Plongmai, K. 2004b. Characteristics of hornbill-dispersed fruits in a tropical seasonal forest in Thailand. *Bird Conservation International*, 14, S81-S88.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T. & Noma, N. 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133, 559-572.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Noma, N., Maruhashi, T. & Wohandee, P. 2005. Fruit-frugivore interactions in a moist evergreen forest of Khao Yai National Park in Thailand. *Tropics*, 14, 345-355.

Kitamura, S., Yumoto, T., Poonswad, P. & Wohandee, P. 2007. Frugivory and seed dispersal by Asian elephants, *Elephas maximus*, in a moist evergreen forest of Thailand. *Journal of Tropical Ecology*, 23, 373-376.

Koike, S., Kasai, S., Yamazaki, K. & Furubayashi, K. 2008. Fruit phenology of *Prunus jamasakura* and the feeding habit of the Asiatic black bear as a seed disperser. *Ecological Research*, 23, 385-392.

Koike, S., Masaki, T., Nemoto, Y., Kozakai, C., Yamazaki, K., Kasai, S., Nakajima, A. & Kaji, K. 2011. Estimate of the seed shadow created by the Asiatic black bear *Ursus thibetanus* and its characteristics as a seed disperser in Japanese cool-temperate forest. *Oikos*, 120, 280-290.

Kozakai, C., Yamazaki, K., Nemoto, Y., Nakajima, A., Koike, S., Abe, S., Masaki, T. & Kaji, K. 2011. Effect of mast production on home range use of Japanese black bears. *The Journal of Wildlife Management*, 75, 867-875.

Krishnamani, R. 1994. Diet composition of the bonnet macaque (*Macaca radiata*) in a tropical dry evergreen forest of Southern India *Tropical Biodiversity*, 2, 285-302.

Kumar, R. S., Mishra, C. & Sinha, A. 2007. Foraging ecology and time-activity budget of the Arunachal macaque *Macaca munzala* – A preliminary study. *Current Science*, 93, 532-539.

Kurup, G. U. & Kumar, A. 1993. Time budget and activity patterns of the lion-tailed macaque (*Macaca silenus*). *International Journal of Primatology*, 14, 27-39.

Lambert, J. E. 1999. Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *American Journal of Physical Anthropology*, 109, 365-386.

Lambert, J. E. 2010. Primate seed dispersers as umbrella species: a case study from Kibale National Park, Uganda, with implications for Afrotropical forest conservation. *American Journal of Primatology*, 71, 1-16.

Lambert, J. E. & Chapman, C. A. 2005. The fate of primate-dispersed seeds: deposition pattern, dispersal distance and implications for conservation. In: *Seed Fate - Predation, Dispersal and Seedling Establishment* (Ed. by Forget, P.-M., Lambert, J. E., Hulme, P. E. & Vander Wall, S. B.), pp. 137-150. Cambridge: CAB International.

Lindburg, D. G. 1977. Feeding behaviour and diet of rhesus monkeys (*Macaca mulatta*) in a Siwalik forest in north India. In: *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes* (Ed. by Clutton-Brock, T. H.), pp. 223-249. London: Academic Press.

Loiselle, B. A., Blendinger, P. G., Blake, J. G. & Ryder, T. B. 2007. Ecological redundancy in seed dispersal systems: a comparison between manakins (Aves: Pipridae) in two tropical forests. In: *Seed dispersal: theory and its application in a changing world* (Ed. by Dennis, A. J., Schupp, E. W., Green, R. A. & Westcott, D. A.). Wallingford, UK: CAB International.

Lucas, P. W. & Corlett, R. T. 1998. Seed dispersal by long-tailed macaques. *American Journal of Primatology*, 45, 29-44.

Makwana, S. C. 1978. Field ecology and behaviour of the rhesus macaque (*Macaca mulatta*): I. Group composition, home range, roosting sites, and foraging routes in the Asarori Forest. *Primates*, 19, 483-492.

Martínez, I., García, D. & Obeso, J. R. 2008. Differential seed dispersal patterns generated by a common assemblage of vertebrate frugivores in three fleshy-fruited trees. *Ecoscience*, 15, 189-199.

Maruhashi, T. 1980. Feeding behavior and diet of the Japanese monkey (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, 21, 141-160.

McConkey, K. R. 2000. Primary seed shadow generated by gibbons in the rain forests of Barito Ulu, central Borneo. *American Journal of Primatology*, 52, 13-29.

McConkey, K. R. & Brockelman, W. Y. 2011. Non-redundancy in the dispersal network of a generalist tropical forest tree. *Ecology*, 92, 1492-1502.

Medellin, R. A. & Gaona, O. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica*, 31, 478-485.

Melo, F. P. L., Martínez-Salas, E., Benítez-Malvido, J. & Ceballos, G. 2010. Forest fragmentation reduces recruitment of large-seeded tree species in a semi-deciduous tropical forest of southern Mexico. *Journal of Tropical Ecology*, 26, 35-43.

Murali, K. S. 1997. Patterns of seed size, germination and seed viability of tropical tree species in southern India. *Biotropica*, 29, 271-279.

Murray, P. 1975. The role of cheek pouches in cercopithecine monkey adaptative strategy. In: *Primate functional morphology and evolution* (Ed. by Tuttle, R. H.), pp. 151-194. The Hague: Mouton.

Nakashima, Y. N. & Sukor, J. A. S. 2009. Importance of common palm civets (*Paradoxurus hermaphroditus*) as a long-distance disperser for large-seeded plants in degraded forests. *Tropics*, 18, 221-229.

Nathan, R. & Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, 15, 278-285.

Ngoprasert, D., Reed, D. H., Steinmetz, R. & Gale, G. A. in revision. Density estimation of Asian bears using chest mark based photographic capture-recapture sampling. *Ursus*.

Noma, N. & Yumoto, T. 1997. Fruiting phenology of animal-dispersed plants in response to winter migration of frugivores in a warm temperate forest on Yakushima Island, Japan. *Ecological Research*, 12, 119-129.

Nuñez-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, 348-354.

O'Brien, T. G. & Kinnaird, M. F. 1997. Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology*, 18, 321-351.

Otani, T. 2004. Effects of macaque ingestion on seed destruction and germination of a fleshy-fruited tree, *Eurya emarginata*. *Ecological Research*, 19, 495-501.

Parrotta, J. A., Knowles, O. H. & Wunderle Jr, J. M. 1997. Development of floristic diversity in 10-years-old reforestation forests on a bauxite mined site in Amazonia. *Forest Ecology and Management*, 99, 21-42.

Peres, C. A. & van Roosmalen, M. 2002. Primate frugivory in two species-rich Neotropical forests: implications for the demography of large-seeded plants in overhunted areas. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.). New York: CAB International.

Pombo, A. R., Waltert, M., Mansjoer, S. S., Mardiastuti, A. & Mühlenberg, M. 2004. Home range, diet and behaviour of the Tonkean macaque (*Macaca tonkeana*) in Lore Lindu National Park, Sulawesi. In: *Land use, nature conservation and the stability of rainforest margins in southeast Asia* (Ed. by Gerold, G., Fremerey, M., Guhardja, E.), pp. 313-325. Berlin, Heidelberg: Springer.

Poulsen, J. R., Clark, C. J., Connor, E. F. & Smith, T. B. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology*, 83, 228-240.

Poulsen, J. R., Clark, C. J. & Smith, T. B. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology*, 17, 787-808.

Priston, N. E. C. 2005. Crop-raiding by *Macaca Ochreata Brunnescens* in Sulawesi: reality, perceptions and outcomes for conservation, University of Cambridge

Rabinowitz, A. R. 1991. Behaviour and movements of sympatric civet species in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Journal of Zoology*, 223, 281-298.

Ramachandran, K. K. & Joseph, G. K. 2000. Habitat utilization of lion-tailed macaque (*Macaca silenus*) in Silent Valley National Park, Kerala, India. *Primate Report*, 58, 17-25.

Riley, E. P. 2007. Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. *International Journal of Primatology*, 28, 107-133.

Rodman, P. S. 1979. Skeletal differentiation of *Macaca fascicularis* and *Macaca nemestrina* in relation to arboreal and terrestrial quadrupedalism. *American Journal of Physical Anthropology*, 51, 51-62.

Rowe, N. & Myers, M. 2011. All the World's Primates. www.alltheworldsprimates.org. Primate Conservation Inc. Charlestown RI. Downloaded on 10/10/2011. Charlestown RI.

Russo, S. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia*, 136, 80-87.

Savini, T. 2005. Socioecology and reproduction in white-handed gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand. PhD thesis, Université de Liège.

Savini, T. & Kanwatanakid-Savini, C. 2011. Feeding overlap and seed dispersal efficiency between sympatric hornbills and gibbons in Thailand. *The Raffles Bulletin of Zoology*, 24, 115-122.

Schülke, O., Pesek, D., Whitman, B. J. & Ostner, J. 2011. Ecology of Assamese macaques (*Macaca assamensis*) at Phu Khieo Wildlife Sanctuary, Thailand. *Journal of Wildlife in Thailand*, 18.

Schupp, E. W., Jordano, P. & Gómez, J. M. 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist*, 188, 333-353.

Sinha, A. 2001. The bonnet macaque revisited: ecology, demography and behaviour. *ENVIS Bulletin: Wildlife and Protected Areas*, 1, 30-39.

Son, V. D. 2003. Diet of *Macaca fascicularis* in a mangrove forest, Vietnam. *Laboratory Primate Newsletter*, 42, 1-5.

Spiegel, O. & Nathan, R. 2007. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters*, 10, 718-728.

Srivastava, A. 2006. Conservation of threatened primates of Northeast India. *Primate Conservation*, 20, 107-113.

Stoner, K. E. & Henry, M. 2008. Seed dispersal and frugivory in tropical ecosystems. In: *Encyclopedia of Life Support Systems*. Oxford: Eolss Publishers.

Su, H.-H. & Lee, L.-L. 2001. Food habits of formosan rock macaques (*Macaca cyclopis*) in Jentse, Northeastern Taiwan, assessed by fecal analysis and behavioral observation. *International Journal of Primatology*, 22.

Sukumar, R. 2006. A brief review of the status, distribution and biology of wild Asian elephants *Elephas maximus*. *International Zoo Yearbook*, 40, 1-8.

Terborgh, J., Nuñez-Iturri, G., Pitman, N. C. A., Cornejo Valverde, F. H., Alvarez, P., Swamy, V., Pringle, E. G. & Paine, C. E. T. 2008. Tree recruitment in an empty forest. *Ecology*, 89, 1757-1768.

Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics*, 1/2, 151-190.

Tsuji, Y. 2010. Effects of the physical characteristics of seeds on gastrointestinal passage time in captive Japanese macaques. *Journal of Zoology*, 280, 171-176.

Tsujino, R. & Yumoto, T. 2009. Topography-specific seed dispersal by Japanese macaques in a lowland forest on Yakushima Island, Japan. *Journal of Animal Ecology*, 78, 119-125.

Umapathy, G. & Kumar, A. 2000. Impacts of the habitat fragmentation on time budget and feeding ecology of lion-tailed macaque (*Macaca silenus*) in rain forest fragments of Anamalai Hills, South India. *Primate Report*, 58, 67-82.

Weir, J. E. S. & Corlett, R. T. 2007. How far do birds disperse seeds in the degraded tropical landscape of Hong Kong, China? *Landscape Ecology*, 22, 131-140.

Wheatley, B. P. 1980. Feeding and ranging of East Bornean *Macaca fascicularis*. In: *The macaques: studies in ecology, behavior and evolution* (Ed. by Lindburg, D. G.), pp. 215-246. New York: Van Nostrand Reinhold Company.

Whitington, C. 1990. Seed dispersal by white-handed gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand. MSc thesis, Mahidol University.

Wrangham, R. W., Chapman, C. A. & Chapman, L. J. 1994. Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology*, 10, 355-368.

1. Summary

1. Summary

Today most South-East Asian countries are aware of the alarming state of their forests. Unfortunately, this deforestation goes hand in hand with the demographic and economic development of these countries (Wright 2005). This represents a strong dilemma which delays authorities in their decisions about an urgent need of protection. In this confrontation between economy and nature, the compromise is difficult to find. However, there are effective solutions. Thailand, in particular, decided, at least in theory, to protect most of its remaining natural forest by creating several large natural parks and to rehabilitate degraded forests by promoting reforestation programmes (Forest Restoration Research Unit 2008; Kashio 2000). However, for effective forest protection and reforestation, it is also necessary to understand how forest regeneration works. Indeed, one aim of this study was to bring a contribution to the knowledge of **a crucial step of forest regeneration: seed dispersal**, in primary as well as secondary forest.

However, even with protected areas and the knowledge of forest maintenance and reforestation processes, the conservation of forests and wildlife cannot work without the cooperation of local communities (Kashio 2000). That's why the other goal of my study was to **make people understand the importance northern pigtailed macaques** could have for the conservation of tropical rainforests. Thailand is very devoted to its forest but I could observe many cases of conflict between humans and macaques, even in the park. By showing the necessity of **macaques to forests, as seed dispersers**, it would be easier to stimulate people to protect them.

At the beginning of our study, little was known about northern pigtailed macaques. Our aim was to highlight their importance on seed dispersal and thus on forest regeneration by studying (1) how their eco-ethological characteristics could make them effective dispersers, from a quantitative and a qualitative point of view, (2) how the influence of biotic factors, such as resources and predation, on their activities and movements may impact their seed dispersal effectiveness, and (3) what particular role they could have in a seed dispersal assemblage.

We showed that northern pigtailed macaques are **effective seed dispersers** for many plant species as they disperse many seeds of many fruit species, of all kind of size, in all forest types, from primary forest to secondary forest, thanks to various handling techniques, and with a neutral effect on the seed germination and viability of most plant species (**Chapter 2**).

Then we showed that northern pigtailed macaques **adapt their ranging pattern** according to fruit availability. Moreover, during fruit scarcity, they shift their diet from frugivorous to omnivorous with an important part of human food, thus described as fallback food (**Chapter 3**). However, **human food does not seem to have important negative consequences on seed dispersal**.

We also described **sleeping sites** characteristics and pre-sleep behavior in northern pigtailed macaques and showed that they were influenced by the **proximity of resources** and the **risk of predation** (**Chapter 4**). Given the fact macaques use few sleeping sites, defecate when they wake up and that all troop members sleep concentrated in a small area, we think that they must create a high seed density below the sleeping trees. This may be harmful for some seed species, but may be beneficial for the ecosystem.

Finally, we showed that, given the seed dispersal service northern pigtailed macaques provide, they seem to be less necessary to the ecosystem than other dispersers. However, they play an **important role as seed dispersal complement** and could become necessary in case of forest degradation as, like for most cercopithecines, their high dietary and behavioral flexibility could enable them to adapt better than other dispersers to a poorer environment (Corlett 1998) (**Chapter 5**).

2. Outlook

2. Outlook

2.1 Conservation implications

Macaques' natural capacity to disperse seeds in various forest types is very important as it could be used to **reforest degraded areas** (Duncan & Chapman 2002; Forest Restoration Research Unit 2006, 2008). Indeed, to know the plant species consumed by macaques would make possible to attract these dispersers in areas requiring reforestation. Only some "attracting" framework species would require to be planted. The other species would be brought naturally by seed dispersers (Forest Restoration Research Unit 2006; Wunderle 1997). In consequences, associations in charge of reforestation programmes could save a lot of money as restoration strategies using such natural processes are already thought to be the most widely applicable and affordable (Corlett & Hau 2000; Duncan & Chapman 2002).

We have to keep in mind that forest protection is not only necessary for forest-dwelling animal species, but also for humans. With the loss of the whole forest, humans could undergo the loss of important resources. The presence of primates in forests is important not only for the regeneration of the forest generally speaking, but also for the **regeneration of resources essential to humans** (Chivian 2002; King 1996; Koné et al. 2008; Millennium Ecosystem Assessment 2005).

2.2 Directions for future research

Although we claimed that northern pigtailed macaques were important seed dispersers in Khao Yai National Park, our study lacks important information on **seed post-dispersal fate**, including suitability of defecation site and probability of germination and seedling establishment *in situ*. These data seem necessary to confirm the seed dispersal status of *M. leonina*. However, they are highly dependent on the probability of secondary dispersal and predation which may be variable according to time and place. Our aim was to determine the "basal" seed dispersal effectiveness of *M. leonina*, but we admit that this may be secondarily influenced by other factors depending on dispersal time and place. Indeed, several authors have shown that initial seed deposition was highly likely to be altered due to post-dispersal processes (Chapman & Russo 2007; Lambert 2001; Lambert 2002). That's why we think that follow-up studies are needed to consider the impact of secondary dispersers and predators on seed fate after dispersal by macaques.

Then, it would be interesting to see the impact of northern pigtailed macaques on some important plant species' **seed shadow** (*i.e.* the spatial distribution of a plant's seeds). Our study enabled us to collect all data necessary for this analysis, except gut retention time, which is expected to be estimated soon in captive pigtailed macaques.

As we have seen in the chapters 1 and 5, many **cercopithecines** species could have an important role in seed dispersal, particularly in degraded areas. It is thus necessary to study these species deeply to know how to protect them and how they could help in reforestation programmes, all the more that some species could even be umbrella species (Lambert 2010) and induce the collateral protection of other species, lesser known but nevertheless important for the ecosystem.

Finally, our study concerns only a single troop of pigtailed macaques, whose home range is characterized by a close proximity to human settlements. This singularity makes it difficult to generalize our results to other troops or populations, and to the species. The study of troops, living in more **remote areas**, will be needed to obtain a more comprehensive knowledge of *M. leonina*.

2.3 Recommendations for Khao Yai National Park

Given its important role in seed dispersal and thus in forest regeneration, it is necessary to protect the vulnerable (IUCN 2011) *M. leonina* wherever it lives. In Khao Yai National Park, the main source of human-macaques' conflicts is food robbery. Thus the best way to stop conflicts would be that macaques learn that they cannot steal food anymore, which could be done through several ways:

1) People should be educated (*e.g.* the head of the park should pass on the message and explain things carefully to every local people; more notice boards should be placed in the way of tourists to inform them *etc.*):

2) Feeding by people should be forbidden: intentional feeding by tourists as well as feeding by local people throwing the remaining of their food on the ground near the houses and the restaurant. These behaviors attract macaques and encourage robbery. Macaques are

thus only seen as thieves by local people and human-macaques' conflicts may have, in the long term, a negative impact on their conservation.

3) Harmful behaviors, such as shooting at macaques with catapults or pellet guns (often observed around the houses of local people) should be punished. These behaviors are bad consequences of the conflict between macaques and local people.

4) To reduce robbery and thus conflicts, local people and tourists should pay attention in food storage: never let food outside, always close doors and windows, close cars, store food in closed cupboards *etc*.

LITERATURE CITED

Agetsuma, N. & Nakagawa, N. 1998. Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. *Primates*, 39, 275-289.

Agetsuma, N. & Noma, N. 1995. Rapid shifting of foraging pattern by Yakushima macaques (*Macaca fuscata yakui*) response to heavy fruiting of *Myrica rubra*. *International Journal of Primatology*, 16, 247-260.

Agostini, I., Holzmann, I. & Bitetti, M. S. D. 2010. Ranging patterns of two syntopic howler monkey species (*Alouatta guariba* and *A. caraya*) in northeastern Argentina. *International Journal of Primatology*, 31, 363-381.

Albert, A., Savini, T. & Huynen, M. C. 2011. Sleeping site selection and presleep behavior in wild pigtailed macaques. *American Journal of Primatology*, 73, 1222-1230.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, 49, 227-267.

Altmann, S. A. & Altmann, J. 1970. *Baboon ecology: African field research*. Basel: Karger.

Altmann, J. & Muruthi, P. 1988. Differences in daily life between semiprovisioned and wild-feeding baboons. *American Journal of Primatology*, 15, 213-221.

Anderson, J. R. 1984. Ethology and ecology of sleep in monkeys and apes. *Advances in the Study of Behavior*, 14, 156-229.

Anderson, J. R. 1998. Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *American Journal of Primatology*, 46, 63-75.

Anderson, J. R. 2000. Sleep-related behavioural adaptations in free-ranging anthropoid primates. *Sleep Medicine Reviews*, 4, 355-373.

Anderson, J. R. & McGrew, W. C. 1984. Guinea baboons (*Papio papio*) at a sleeping site. *American Journal of Primatology*, 6, 1-14.

Andresen, E. 1999. Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. *Biotropica*, 31, 145-158.

Andresen, E. 2002. Primary seed dispersal by red howler monkeys and the effect of defecation patterns on the fate of dispersed seeds. *Biotropica*, 34, 261-272.

Andresen, E. & Levey, D. J. 2004. Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia*, 139, 45-54.

Asensio, N., Brockelman, W. Y., Malaivijitnond, S. & Reichard, U. H. 2011. Gibbon travel paths are goal oriented. *Animal Cognition*, 14, 395-405.

Astaras, C. & Waltert, M. 2010. What does seed handling by the drill tell us about the ecological services of terrestrial cercopithecines in African forests? *Animal Conservation*, 13, 568-578.

Aureli, F., Shaffner, C., Boesch, C., Bearder, S., Call, J., Chapman, C., Connor, R., Di Fiore, A., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P. C., Lehmann, J., Manson, J. H., Ramos-Fernández, G., Strier, K. B. & van Schaik, C. P. 2008. Fission-fusion dynamics: new research frameworks. *Current Anthropology*, 49, 627-654.

Babweteera, F., Savill, P. & Brown, N. 2007. *Balanites wilsoniana*: Regeneration with and without elephants. *Biological Conservation*, 134, 40-47.

Balcomb, S. R. & Chapman, C. A. 2003. Bridging the gap: influence of seed deposition on seedling recruitment in a primate-tree interaction. *Ecological Monographs*, 73, 625-642.

Barbour, M. G., Burk, J. H., Pitts, W. D., Gilliam, F. S. & Schwartz, M. W. 1999. *Terrestrial plant ecology*, Third edn. Menlo Park, CA: The Benjamin/Cummings Plublishing Company, Inc.

Barrett, A. S. 2005. Foraging ecology of the vervet monkey (*Chlorocebus aethiops*) in mixed lowveld bushveld and sour lowveld bushveld of the Blydeberg Conservancy, Northern Province, South Africa. Magister thesis, University of South Africa.

Barrett, A. S. 2009. Spatial and temporal patterns in resource dispersion and the structure of range use and co-existence in a social omnivore *Chlorocebus aethiops*. PhD thesis, University of South Africa.

Bascompte, J. & Jordano, P. 2006. The structure of plant-animal mutualistic networks. In: *Ecological networks* (Ed. by Pascual, M. & Dunne, J.), pp. 143-159. Oxford, US: Oxford University Press.

Bascompte, J., Jordano, P., Melián, C. J. & Olesen, J. M. 2003. The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100, 9383-9387.

Baskin, C. C. & Baskin, J. M. 2000. *Seeds: ecology, biogeography, and evolution of dormancy and germination*. London: Academic Press.

Benitez-Malvido, J. 2006. Effect of low vegetation on the recruitment of plants in successional habitat types. *Biotropica*, 38, 171-182.

Bleher, B. 2000. Seed dispersal and frugivory: ecological consequences for tree populations and bird communities, Fakultät für Mathematik, Informatik und Naturwissenschaften.

Blom, A., Zalinge, R. v., Heitkönig, I. M. A. & Prins, H. H. T. 2005. Factors influencing the distribution of large mammals within a protected central African forest. *Oryx*, 39, 381-388.

Boon, P. P. & Corlett, R. 1989. Seed dispersal by the lesser short-nosed fruit bat (*Cynopterus brachyotis,* Pteropodidae, Megachiroptera). *Malayan Nature Journal*, 42, 251-256.

Boonratana, R. 2000. Ranging behavior of proboscis monkeys (*Nasalis larvatus*) in the Lower Kinabatangan, Northern Borneo. *International Journal of Primatology*, 21, 497-518.

Borries, C., Larney, E., Kreetiyutanont, K. & Koenig, A. 2002. The diurnal primate community in a dry evergreen forest in Phu Khieo wildlife sanctuary, Northeast Thailand. *Natural History Bulletin of the Siam Society*, 50, 75-88.

Boulton, A. M., Horrocks, J. A. & Baulu, J. 1996. The Barbados vervet monkey (*Cercopithecus aethiops sabaeus*): changes in population size and crop damage, 1980-1994. *International Journal of Primatology*, 17, 831-844.

Bourgoin, G. 2008. Etude des variations spatio-temporelles de l’activité et de l’utilisation des ressources par les herbivores. PhD thesis, Université Claude Bernard.

Brennan, E. J. 1985. De Brazza's monkeys (*Cercopithecus neglectus*) in Kenya: Census, distribution, and conservation. *American Journal of Primatology,* 8, 269-277.

Brito, J. C. 2003. Seasonal variation in movements, home range and habitat use by male *Vipera latastei* in Northern Portugal. *Journal of herpetology*, 37, 155-160.

Brockelman, W. Y. 1998. Long term ecological research plot for the study of animals diets in Khao Yai National Park. In: *The Asian Hornbills: Ecology and Conservation. Thai Studies in Biodiversity 2* (Ed. by Poonsawad, P.), pp. 307-310. Bangkok: Biodiversity Research and Training Program, National Center for Genetic Engineering and Biotechnology with support from the Thailand Research Fund in collaboration with Science Society of Thailand.

Brockman, D. K. & van Schaik, C. P. 2005. *Seasonality in primates - Study of living and extinct human and non-human primates*. Cambridge: Cambridge University Press.

Brodie, J. F. 2007. Effects of seed dispersal by gibbons, sambar, and muntjac on *Choerospondias axillaris* demography, and the disruption of this mutualism by wildlife poaching. PhD, University of Montana.

Brodie, J. F., Helmy, O. E., Brockelman, W. Y. & Maron, J. L. 2009. Functional differences within a guild of tropical mammalian frugivores. *Ecology*, 90, 688-698.

Bronikowski, A. M. & Altmann, J. 1996. Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behavioral Ecology and Sociobiology*, 39, 11-25.

Brook, B. W., Sodhi, N. S. & Ng, P. K. L. 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature*, 424, 420-423.

Brotcorne, F., Wandia, I. N., Rompis, A. L. T., Soma, I. G., Suartha, I. N. & Huynen, M. C. 2011. Recent demographic and behavioural data of *Macaca fascicularis* at Padangtegal, Bali (Indonesia). In: *Monkeys on the edge: ecology and management of long-tailed macaques and their interface with humans* (Ed. by Gumert, M. D., Fuentes, A. & Jones-Engel, L.), pp. 180-183. Cambridge Cambridge University Press.

Busse, C. 1980. Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve. *Botswana Notes and Records*, 12, 15-21.

Butler, R. A. & Laurance, W. F. 2008. New strategies for conserving tropical forests. *Trends in Ecology and Evolution*, 23, 469-472.

Buzzard, P. J. 2006. Cheek pouch use in relation to interspecific competition and predator risk for three guenon monkeys (*Cercopithecus* spp.). *Primates*, 47, 336-341.

Cain, M. L., Milligan, B. G. & Strand, A. E. 2000. Long-distance seed dispersal in plant populations *American Journal of Botany*, 87, 1217-1227.

Caine, N. G. 1987. Vigilance, vocalizations, and cryptic behavior at retirement in captive groups of red-bellied tamarins (*Saguinus labiatus*). *American Journal of Primatology*, 12, 241-250.

Caldecott, J. O. 1986. *An ecological and behavioural study of the pig-tailed macaque*. Basel: Karger.

Caldecott, J. O., Feistner, A. T. C. & Gadsby, E. L. 1996. A comparison of ecological strategies of pig-tailed macaques, mandrills and drills. In: *Evolution and ecology of macaque societies* (Ed. by Fa, J. E. & Lindburg, D. G.), pp. 73-94. Cambridge Cambridge University Press.

Campos-Arceiz, A., Larrinaga, A. R., Weerasinghe, U. R., Takatsuki, S., Pastorini, J., Leimgruber, P., Fernando, P. & Santamaría, A. L. 2008. Behavior rather than diet mediates seasonal differences in seed dispersal by Asian elephants. *Ecology*, 89, 2684-2691.

Chang, K. 1999. Foraging strategies of Formosan macaques (*Macaca cyclopis*) in Fushan Experimental Forest. Dissertation, National Taiwan University.

Chanthorn, W. & Brockelman, W. Y. 2008. Seed dispersal and seedling recruitment in the light-demanding tree *Choerospondias axillaris* in old-growth forest in Thailand. *ScienceAsia*, 34, 129-135.

Chapman, C. A. 1987. Flexibility in diets of three species of Costa Rican primates. *Folia primatologica*, 49, 90-105.

Chapman, C. A. 1988. Patterns of foraging and range use by three species of neotropical primates. *Primates*, 29, 177-194.

Chapman, C. A. 1989. Primate seed dispersal: The fate of dispersed seeds. *Biotropica*, 21, 148-154.

Chapman, C. A. 1989. Spider monkey sleeping sites: Use and availability. *American Journal of Primatology*, 18, 53-60.

Chapman, C. A. 1995. Primate seed dispersal: Coevolution and conservation implications. *Evolutionary Anthropology*, 4, 74-82.

Chapman, C. A. & Chapman, L. J. 1990. Dietary variability in primate populations. *Primates*, 31, 121-128.

Chapman, C. A. & Chapman, L. J. 1995. Survival without dispersers: seeding recruitment under parents. *Conservation Biology*, 9, 675-678.

Chapman, C. A. & Chapman, L. J. 1996. Frugivory and the fate of dispersed and nondispersed seeds in six African tree species. *Journal of Tropical Ecology*, 12, 491-504.

Chapman, C. A. & Chapman, L. J. 1999. Forest restoration in abandoned agricultural land: A case study from East Africa. *Conservation Biology*, 13, 1301-1311.

Chapman, C. A. & Chapman, L. J. 2000. Determinants of group size in primates: the importance of travel costs. In: *On the move: How and why animals travel in groups* (Ed. by Boinski, S. & Garber, P. A.), pp. 24-42. Chicago University of Chicago Press.

Chapman, C. A., Chapman, L. J. & McLaughlin, R. L. 1989. Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. *Oecologia*, 79, 506-511.

Chapman, C. A., Chapman, L. J., Vulinec, K., Zanne, A. & Lawes, M. J. 2003. Fragmentation and alteration of seed dispersal processes: an initial evaluation of dung beetles, seed fate, and seedling diversity. *Biotropica*, 35, 382-393.

Chapman, C. A., Chapman, L. J., Wrangham, R., Hunt, K., Gebo, D. & Gardner, L. 1992a. Estimators of fruit abundance of tropical trees. *Biotropica*, 24, 527-531.

Chapman, C. A., Lawes, M. J. & Eeley, H. A. C. 2006. What hope for African primate diversity? *African Journal of Ecology*, 44, 116-133.

Chapman, C. A. & Onderdonk, D. A. 1998. Forests without primates: Primate/plant codependency. *American Journal of Primatology*, 45, 127-141.

Chapman, C. A. & Russo, S. E. 2007. Primate seed dispersal: Linking behavioral ecology with forest community structure. In: *Primates in perspective* (Ed. by Campbell, C. J., Fuentes, A. F., MacKinnon, K. C., Panger, M. & Bearder, S.), pp. 510-525. Oxford: Oxford University Press.

Chapman, H. M., Goldson, S. L. & Beck, J. 2009. Postdispersal removal and germination of seed dispersed by *Cercopithecus nictitans* in a West African montane forest. *Folia primatologica*, 81, 41-50.

Chapman, L. J., Chapman, C. A. & Wrangham, R. 1992b. *Balanites wilsoniana*: elephant dependent dispersal? *Journal of Tropical Ecology*, 8, 275-283.

Chauhan, A. & Pirta, R. S. 2010. Agonistic interactions between humans and two species of monkeys (rhesus monkey *Macaca mulatta* and hanuman langur *Semnopithecus entellus*) in Shimla, Himachal Pradesh. *Journal of Psychology*, 1, 9-14.

Chaves, Ó. M., Stoner, K. E., Arroyo-Rodríguez, V. & Estrada, A. 2011. Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rain forests in southern Mexico. *International Journal of Primatology*, 32, 177-192.

Chen, C. E. 1999. The influence of Formosan macaques (*Macaca cyclopis*) on seed dispersal in Fushan experimental forest M.S. thesis, National Taiwan University.

Chivian, E. 2002. *Biodiversity: its importance to human health, interim execuative summary*. Boston: MA:Center for Health and the Global Environment, Harvard Medical School.

Choudhury, A. 2003. The pig-tailed macaque *Macaca nemestrina* in India - Status and conservation. *Primate Conservation*, 19, 91-98.

Choudhury, A. 2008. Ecology and behaviour of the Pig-tailed macaque *Macaca nemestrina leonina* in some forests of Assam in north-east India. . *Journal of the Bombay Natural History Society*, 105, 279-291.

Cipollini, M. L. & Levey, D. J. 1997. Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *The American Naturalist*, 150, 346-372.

Clark, D. A. & Clark, D. B. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *The American Naturalist*, 124, 769-789.

Clark, C. J., Poulsen, J. R. & Parker, V. T. 2001. The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. *Biotropica*, 33, 606-620.

Clutton-Brock, T. H. & Harvey, P. H. 1977. Species differences in feeding and ranging behaviour in primates. In: *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes* (Ed. by Clutton-Brock, T. H.), pp. 557-584. London: Academic Press.

Coates-Estrada, R. & Estrada, A. 1988. Frugivory and seed dispersal in *Cymbopetalum baillonii* at Los Tuxtlas, Mexico. *Journal of Tropical Ecology*, 4, 157-172.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of populations* (Ed. by den Boer, P. J. & Gradwell, G. R.), pp. 298-312. Wageningen, The Netherlands: Centre for Agricultural Publication and Documentation.

Cordeiro, N. J. & Howe, H. F. 2001. Low recruitment of trees dispersed by animals in African forest fragments. *Conservation Biology*, 15, 1733-1741.

Corlett, R. T. 1994. What is secondary forest? *Journal of Tropical Ecology*, 10, 445-447.

Corlett, R. T. 1996. Characteristics of vertebrate-dispersed fruits in Hong Kong. *Journal of Tropical Ecology*, 12, 819-833.

Corlett, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews*, 73, 413-448.

Corlett, R. T. 2002. Frugivory and seed dispersal in degraded tropical East Asian landscape. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 451-465. New York: CABI Publishing.

Corlett, R. T. 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica*, 39, 292-303.

Corlett, R. T. 2009. Seed dispersal distances and plant migration potential in tropical East Asia. *Biotropica*, 41, 592-598.

Corlett, R. T. & Hau, B. C. H. 2000. Seed dispersal and forest restoration. In: *Forest restoration for wildlife conservation* (Ed. by Elliott, S., Kerby, J., Blakesley, D., Hardwick, K., Woods, K. & Anusarnsunthorn, V.), pp. 317-325. Chiang Mai University, Thailand: International Tropical Timber Organisation and The Forest Restoration Research Unit.

Corlett, R. T. & Lucas, P. W. 1989. Consumption of *Campnospermum auriculatum* (Anacardiaceae) fruit by vertebrates in Singapore. *Malayan Nature journal*, 42, 273-276.

Corlett, R. T. & Lucas, P. W. 1990. Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*). *Oecologia*, 82, 166-171.

Cowlishaw, G. & Dunbar, R. 2000. *Primate conservation biology*. Chicago and London: The University of Chicago Press.

Cramer, J. M., Mesquita, R. C. G. & Williamson, G. B. 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biological Conservation*, 137, 415-423.

Crockett, C. M. & Wilson, W. L. 1980. The ecological separation of *Macaca nemestrina* and *M. fascicularis* in Sumatra. In: *The Macaques: studies in ecology, behavior and evolution* (Ed. by Lindburg, D. G.), pp. 148-181. New York: van Nostrand Rheinhold.

Culot, L. 2009. Primary seed dispersal by two sympatric species of tamarins, *Saguinus fuscicollis* and *Saguinus mystax*, and post-dispersal seed fate, PhD thesis, Université de Liège.

Culot, L., Huynen, M.-C. & Heymann, E. W. 2009. Short-term post-dispersal fate of seeds defecated by two small primate species (*Saguinus mystax* and *Saguinus fuscicollis*) in the Amazonian forest of Peru. *Journal of Tropical Ecology*, 25, 229-238.

Culot, L., Lazo, F. J. J. M., Huynen, M.-C., Poncin, P. & Heymann, E. W. 2010. Seasonal variation in seed dispersal by tamarins alters seed rain in a secondary rainforest. *International Journal of Primatology*, 31, 553-569.

da Silva, J. M. C., Uhl, C. & Murray, G. 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conservation Biology*, 10, 491-503.

Davies, R. G. 1990. Sighting of a clouded leopard (*Neofelis nebulosa*) in a troop of pigtail macaques (*Macaca nemestrina*) in Khao Yai National Park, Thailand. *Natural History Bulletin of the Siam Society*, 28, 95-96.

Day, R. T. & Elwood, R. W. 1999. Sleeping site selection by the golden-handed tamarin *Saguinus midas midas*: the role of predation risks, proximity to feeding sites, and territorial defence. . *Ethology*, 105, 1035-1051.

de Jong, W., Chokkalingam, U., Smith, J. & Sabogal, C. 2001. Tropical secondary forests in Asia: introduction and synthesis. *Journal of Tropical Forest Science*, 13, 563-576.

Delson, E. 1980. Fossil macaques, phyletic relationships and a scenario of deployment. In: *The Macaques: Studies in Ecology, Behavior and Evolution* (Ed. by Linburg, D. G.), pp. 10-30. New York: Van Nostrand Reinhold Company.

Dew, J. L. & Wright, P. 1998. Frugivory and seed dispersal by four species of primates in Madagascar’s Eastern rain forest. *Biotropica*, 30, 425-437.

Di Bitetti, M. S., Vidal, E. M. L., Baldovino, M. C. & Benesovsky, V. 2000. Sleeping site preferences in tufted capuchin monkeys (*Cebus apella nigritus*). *American Journal of Primatology*, 50, 257-274.

Di Fiore, A. 2003. Ranging behavior and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Yasuní National Park, Ecuador. *American Journal of Primatology*, 59, 47-66.

Dirzo, R. 2001. Plant-animal interactions: Lessons for our understanding of nature, and implications for biodiversity conservation. In: *Ecology: Achievement and challenge* (Ed. by Press, M. C., J.Huntley, N. & Levin, S.), pp. 319-355. Oxford, UK: Blackwell Science.

Dittus, W. P. J. 1975. Populationd dynamics of the toque monkey, *Macaca sinica*. In: *Socioecology and psychology of primates* (Ed. by Tuttle, R. H.), pp. 125-151. The Hague: Mouton Publishers.

Dominy, N. J. & Duncan, B. W. 2005. Seed-spitting primates and the conservation and dispersion of large-seeded trees. *International Journal of Primatology*, 26, 631-649.

Donatti, C. I., Guimarães, P. R., Galetti, M., Pizo, M. A., Marquitti, F. M. D. & Dirzo, R. 2011. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecology Letters*, 14, 773-781.

Doran, D. M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P. & Shah, N. 2002. Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling method. *American Journal of Primatology*, 58, 91-116.

Downs, J. A. 2008. Network analysis of animal space-use patterns. PhD thesis, Florida State University.

Dunbar, R. I. M. 1988. *Primate social systems*. London & Sydney: Croom Helm.

Duncan, R. S. & Chapman, C. A. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications*, 9, 998-1008.

Duncan, R. S. & Chapman, C. A. 2002. Limitations of animal seed dispersal for enhancing forest succession on degraded lands. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 437-450. New York: CAB International.

Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P. & Sodhi, N. S. 2009. The sixth mass coextinction: are most endangered species parasites and mutualists? *Proceedings of the Royal Society B*, 276, 3037-3045.

Estrada, A. & Coates-Estrada, R. 1984. Fruit eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxlas, Mexico. *American Journal of Primatology*, 6, 77-91.

Estrada, A. & Coates-Estrada, R. 1996. Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *International Journal of Primatology*, 17, 759-783.

Estrada, A. & Estrada, R. 1976. Establishment of a free-ranging colony of stumptail macaques (*Macaca arctoides*): relations to the ecology. *Primates*, 17, 337-355.

Fam, S. D. & Nijman, V. 2011. *Spizaetus* hawk-eagles as predators of arboreal colobines. *Primates*, 52, 105-110.

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, 153-160.

Fashing, P. J., Mulindahabi, F., Gakima, J.-B., Masozera, M., Mununura, I., Plumptre, A. J. & Nguyen, N. 2007. Activity and ranging patterns of Colobus angolensis ruwenzorii in Nyungwe Forest, Rwanda: possible costs of large group size. *International Journal of Primatology*, 28, 529-550.

Feeroz, M. M., Islam, M. A. & Kabir, M. M. 1994. Food and feeding behaviour of hoolock gibbon (*Hylobates hoolock*), capped langur (*Presbytis pileata*), and pigtailed macaque (*Macaca nemestrina*) of Lawachara. *Bangladesh Journal of Zoology*, 22, 123-132.

Ferguson, S. H., Taylor, M. K., Born, E. W., Rosing-Asvid, A. & Messier, F. 1999. Determinants of home range size for polar bears (*Ursus maritimus*). *Ecology Letters*, 2, 311-318.

Finegan, B. 1996. Pattern and process in neotropical secondary rain forest: the first 100 years of succession. *Tree*, 11, 119-124.

Fleming, T. H. & Heithaus, E. R. 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica*, 13, 45-53.

Fleming, T. H. & Williams, C. F. 1990. Phenology, seed dispersal, and recruitment in *Cecropia peltata* (Moraceae) in Costa Rican tropical dry forest. *Journal of Tropical Ecology*, 6, 163-178.

Foerster, S. & Monfort, S. L. 2010. Fecal glucocorticoids as indicators of metabolic stress in female Sykes' monkeys (*Cercopithecus mitis albogularis*). *Hormones and Behavior*, 58, 685-697.

Fooden, J. 1975. Taxonomy and evolution of liontail and pigtail macaques (Primates: Cercopithecidae). *Fieldiana: Zoology*, 67, 1-168.

Fooden, J. 1980. Classification and distribution of living macaques (*Macaca* Lacépède, 1799). In: *The Macaques: Studies in Ecology, Behavior and Evolution* (Ed. by Lindburg, D. G.), pp. 1-9. New York: Van Nostrand Reinhold Company

Forest Restoration Research Unit. 2000. Tree seeds and seedlings for restoring forests in Northern Thailand. Biology Department, Science Faculty, Chiang Mai University, Thailand.

Forest Restoration Research Unit. 2006. *How to plant a forest: the principles and practice of restoring tropical forests*. Biology Department, Science Faculty, Chiang Mai University, Thailand.

Forest Restoration Research Unit. 2008. *Research for restoring tropical forest ecosystems: A practical guide*. Biology Department, Science Faculty, Chiang Mai University, Thailand.

Forget, P.-M., Dennis, A. J., Mazer, S. J., Jansen, P. A., Kitamura, S., Lambert, J. E. & Westcott, D. A. 2007. Seed allometry and disperser assemblages in tropical rainforests: a comparision of four floras on different continents. In: *Seed dispersal: theory and its application in a changing world* (Ed. by Dennis, A. J., Schupp, E. W., Green, R. J. & Westcott, D.), pp. 5-36. Wallingford, UK: CAB International Publishing.

Forthman-Quick, D. L. 1986. Activity budgets and the consumption of human food in two troops of baboons, *Papio anubis*, at Gilgil, Kenya. In: *Primate ecology and conservation* (Ed. by G., E. J. & C., L. P.), pp. 221-228. Cambridge: Cambridge University Press.

Fortuna, M. A. & Bascompte, J. 2006. Habitat loss and the structure of plant-animal mutualistic networks. *Ecology Letters*, 9, 281-286.

Fukuda, F. 1989. Habitual fission-fusion and social organization of the Hakone troop of Japanese macaques in Kanagawa prefecture, Japan *International Journal of Primatology*, 10, 419-439.

Fukuda, F. 2004. Dispersal and environmental disturbance in japanese macaques (*Macaca fuscata*). *Primate Report*, 68, 53-69.

Fust, P. 2008. Function and use of cheek pouches in cape chacma baboon (*Papio ursinus orientalis*) population in Cape Floral Kingdom, South Africa. Research Dissertation, Napier University.

Ganas, J., Robbins, M. M., Nkurunungi, J. B., Kaplin, B. A. & McNeilage, A. 2004. Dietary variability of mountain gorillas in Bwindi Impenetrable National park, Uganda. *International Journal of Primatology*, 25, 1043-1072.

Ganesh, T. & Davidar, P. 2005. Fruiting phenology and pre-dispersal seed predation in a rainforest in southern western Ghats, India. In: *Tropical fruits and frugivores: The search of strong interactors* (Ed. by Dew, J. L. & Boubli, J.-P.), pp. 139-154. Dordrecht: Springer.

Garber, P. A. 2000. Evidence for the use of spatial, temporal, and social information by primate foragers. In: *On the move: How and why animals travel in groups* (Ed. by Boinski, S. & Garber, P. A.), pp. 261-297. Chicago and London: The University of Chicago Press.

Garber, P. A. & Lambert, J. E. 1998. Introduction to primate seed dispersal. Primates as seed dispersers: ecological processes and directions for future research. *American Journal of Primatology*, 45, 3-8.

Gathua, M. 2000. The effects of primates and squirrels on seed survival of a canopy tree, *Afzeiia quanzensis*, in Arabuko-Sokoke Forest, Kenya. *Biotropica*, 32, 127-132.

Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J. & Wilmers, C. C. 2007. LoCoh: nonparameteric kernel methods for constructing home ranges and utilization distributions. *PloS ONE*, e207.

Gippoliti, S. 2001. Notes on the taxonomy of *Macaca nemestrina leonina* Blyth, 1863 (Primates: Cercopithecidae). *Hystrix Italian Journal of Mammalogy*, 12, 51-54.

Gross-Camp, N. & Kaplin, B. A. 2005. Chimpanzee (*Pan troglodytes*) seed dispersal in an Afromontane forest: microhabitat influences on the postdispersal fate of large seeds. *Biotropica*, 37, 641-649.

Gross-Camp, N. & Kaplin, B. A. 2011. Differential seed handling by two African primates affects seed fate and establishment of large-seeded trees. *Acta Oecologica*, 37, 578-586.

Hamilton, W. J. 1982. Baboon sleeping site preferences and relationships to primate grouping patterns. *American Journal of Primatology*, 3, 41-53.

Hamilton, W. J. & Watt, K. E. F. 1970. Refuging. *Annual Review of Ecology and Systematics*, 1, 263-286.

Hanya, G. 2004. Diet of a Japanese macaque troop in the coniferous forest of Yakushima. *International Journal of Primatology,* 25, 55-71.

Hanya, G. 2005. Comparisons of dispersal success between the species fruiting prior to and those at the peak of migrant frugivore abundance. *Plant Ecology,* 181, 167-177.

Hanya, G., Kiyono, M., Yamada, A., Suzuki, K., Furukawa, M., Yoshida, Y. & Chijiiwa, A. 2006. Not only annual food abundance but also fallback food quality determines the Japanese macaque density: evidence from seasonal variations in home range size. *Primates,* 47, 275-278.

Hanya, G., Noma, N. & Agetsuma, N. 2003. Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima. *Primates*, 44, 51-59.

Harvey, P. H. & Clutton-Brock, T. H. 1981. Primate home-range size and metabolic needs. *Behavioral Ecology and Sociobiology,* 8, 151-155.

Hausfater, G. & Maede, B. J. 1982. Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates,* 23, 287-297.

Herrera, C. M. 1984. A study of avian frugivores, bird-dispersed plants, and their interaction in mediterranean scrublands. *Ecological Monographs*, 54, 1-23.

Herrera, C. M. 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos*, 44, 132-141.

Herrera, C. M. & Jordano, P. 1981. *Prunus mahaleb* and birds: the high-efficiency seed dispersal system of a temperate fruiting tree. *Ecological Monographs*, 51, 203-218.

Heymann, E. W. 1995. Sleeping habits of tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Mammalia, Primates, Callitrichidae), in north-eastern Peru. *Journal of Zoology,* 237, 211-226.

Hill, C. & Webber, A. D. 2010. Perceptions of nonhuman primates in human-wildlife conflict scenarios. *American Journal of Primatology,* 72, 919-924.

Hill, C. M. 2000. Conflict of interest between people and baboons: crop raiding in Uganda. *International Journal of Primatology*, 21, 299-315.

Holl, K. D. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica*, 31, 229-242.

Howe, H. F. 1983. Annual variation in a neotropical seed-dispersal system. In: *Tropical rain forest: ecology and management* (Ed. by Sutton, S. L., Whitmore, T. C. & Chadwick, A. C.), pp. 211-227. Oxford: Blackwell Scientific Publications.

Howe, H. F. 1984. Constraints on the evolution of mutualisms. *The American Naturalist,* 123, 764-777.

Howe, H. F. 1984. Implications of seed dispersal by animals for tropical reserve management. *Biological Conservation*, 30, 261-281.

Howe, H. F. 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia*, 79, 417-426.

Howe, H. F. 2000. No question: Seed dispersal matters. *Trends in Ecology and Evolution*, 15, 434-436.

Howe, H. F. & Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13, 201-228.

Huang, C.-L. 2005. Effects of dispersal via cheek pouches of Formosan macaques (*Macaca cyclopis*) on seed shadow and seed fate of three Lauraceae species at Fushan experimental forest, National Taiwan University.

Humphrey, S. R. & Bain, J. R. 1990. *Endangered animals of Thailand*. Gainesville, Florida: Sandhill Cran Press.

Isbell, L. A. 1983. Daily ranging behavior of red colobus (*Colobus badius tephrosceles*) in Kibale Forest, Uganda *Folia primatologica*, 41, 34-48.

IUCN. 2011. IUCN Red List of Threatened Species. Version 2011.1. http://www.iucnredlist.org Downloaded on 26/10/2011.

Izumiyama, S., Mochizuki, T. & Shiraishi, T. 2003. Troop size, home range area and seasonal range use of the Japanese macaque in the Northern Japan Alps. *Ecological Research*, 18, 465-474.

Janson, C. 2000. Spatial movement strategies: theory, evidence, and challenges. In: *On the move: How and why animals travel in groups* (Ed. by Boinski, S. & Garber, P. A.), pp. 165-203. Chicago: The University of Chicago Press.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist*, 104, 501-528.

Johns, A. D. & Skorupa, J. P. 1987. Responses of rain-forest primates to habitat disturbance: a review. *International Journal of Primatology*, 8, 157-191.

Jordano, P., Bascompte, J. & Olesen, J. M. 2003. Invariant properties in coevolutionary networks of plant-animal interactions. *Ecology Letters*, 6, 69-81.

Jordano, P., García, C., Godoy, J. A. & García-Castaño, J. L. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 3278-3282.

Jordano, P. & Godoy, J. A. 2002. Frugivore-generated seed shadows: a landscape view of demographic and genetic effects. In: *Seed-dispersal and frugivory: ecology, evolution* *and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 305-321. New York: CAB International.

Kanwatanakid, C.-O. 2000. Characteristics of fruits consumed by the white-handed gibbon (*Hylobates lar*) in Khao Yai National Park, Thailand. PhD thesis, Mahidol University.

Kanwatanakid-Savini, C.-O., Poonswad, P. & Savini, T. 2009. An assessment of food overlap between gibbons and hornbills. *The Raffles Bulletin of Zoology*, 57, 189-198.

Kaplin, B. A. 2001. Ranging behavior of two species of guenons (*Cercopithecus lhoesti* and *C. mitis doggetti*) in the Nyungwe Forest Reserve, Rwanda. Inter*national Journal of Primatology*, 22, 521-548.

Kaplin, B. A. & Lambert, J. E. 2002. Effectiveness of seed dispersal by *Cercopithecus* Monkeys: Implications for seed input into degraded areas. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 351-364. New York: CABI Publishing.

Kaplin, B. A. & Moermond, T. C. 1998. Variation in seed handling by two species of forest monkeys in Rwanda. *American Journal of Primatology*, 45, 83-101.

Kaplin, B. A., Munyaligoga, V. & Moermond, T. C. 1998. The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*). *Biotropica*, 30, 56-71.

Kashio, M. 2000. Trends of wildlife conservation in changing forest resource situations in the Asia-Pacific Region. In: *Forest restoration for wildlife conservation* (Ed. by Elliott, S., Kerby, J., Blakesley, D., Hardwick, K., Woods, K. & Anusarnsunthorn, V.). Chiang Mai University, Thailand: International Tropical Timber Organisation and The Forest Restoration Research Unit.

Khamcha, D. 2009. Movement patterns, seed dispersal and tree-fall gap use by a forest interior frugivore: puff-throated bulbul (*Alophoixus pallidus*), Master thesis, King Mongkut's University of Technology Thonburi.

Khamcha, D. & Sukumal, N. 2009. *Python molurus* predation on a *Macaca nemestrina* in Khao Yai National Park, Thailand. *Hamadryad*, 34, 176-178.

King, S. R. 1996. Conservation and tropical medicinal: plant research. In: *Medicinal resources of the tropical forest: biodiversity and its importance to human health* (Ed. by Balick, M. J., Elisabetsky, E. & Laird, S. A.), pp. 63-74. Columbia Columbia University Press

Kirika, J. M., Bleher, B., Böhning-Gaese, K., Chira, R. & Farwig, N. 2008. Fragmentation and local disturbance of forests reduce frugivore diversity and fruit removal in *Ficus thonningii* trees. *Basic and Applied Ecology,* 9, 663-672.

Kitamura, S. 2007. Current knowledge and future issues for frugivory and seed dispersal by animals in Southeast Asia: special reference to large frugivorous birds and mammals. *Japanese Journal of Ecology*, 57, 159-171.

Kitamura, S., Suzuki, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T., Noma, N. & Suckasam, C. 2006. Dispersal of *Canarium euphyllum* (Burseraceae), a large-seeded tree species, in a moist evergreen forest in Thailand. *Journal of Tropical Ecology*, 22, 137-146.

Kitamura, S., Suzuki, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Noma, N., Maruhashi, T. & Suckasam, C. 2004a. Dispersal of *Aglaia spectabilis*, a large-seeded tree species in a moist evergreen forest in Thailand. *Journal of Tropical Ecology*, 20, 421-427.

Kitamura, S., Yumoto, T., Noma, N., Chuailua, P., Maruhashi, T., Wohandee, P. & Poonswad, P. 2008. Aggregated seed dispersal by wreathed hornbills at a roost site in a moist evergreen forest of Thailand. *Ecological Research*, 23, 943-952.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P. & Plongmai, K. 2004b. Characteristics of hornbill-dispersed fruits in a tropical seasonal forest in Thailand. *Bird Conservation International*, 14, S81-S88.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T. & Noma, N. 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133, 559-572.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Noma, N., Maruhashi, T. & Wohandee, P. 2005. Fruit-frugivore interactions in a moist evergreen forest of Khao Yai National Park in Thailand. *Tropics*, 14, 345-355.

Kitamura, S., Yumoto, T., Poonswad, P. & Wohandee, P. 2007. Frugivory and seed dispersal by Asian elephants, *Elephas maximus*, in a moist evergreen forest of Thailand. *Journal of Tropical Ecology*, 23, 373-376.

Knogge, C., Herrera, E. R. T. & Heymann, E. W. 2003. Effects of passage through tamarin guts on the germination potential of dispersed seeds. *International Journal of Primatology*, 24, 1121-1128.

Koike, S., Kasai, S., Yamazaki, K. & Furubayashi, K. 2008. Fruit phenology of *Prunus jamasakura* and the feeding habit of the Asiatic black bear as a seed disperser. *Ecological Research*, 23, 385-392.

Koike, S., Masaki, T., Nemoto, Y., Kozakai, C., Yamazaki, K., Kasai, S., Nakajima, A. & Kaji, K. 2011. Estimate of the seed shadow created by the Asiatic black bear *Ursus thibetanus* and its characteristics as a seed disperser in Japanese cool-temperate forest. *Oikos*, 120, 280-290.

Koné, I., Lambert, J. E., Refisch, J. & Bakayoko, A. 2008. Primate seed dispersal and its potential role in maintaining useful tree species in the Taï region, Côte-d'Ivoire: implications for the conservation of forest fragments. *Tropical Conservation Science*, 1, 293-306.

Kozakai, C., Yamazaki, K., Nemoto, Y., Nakajima, A., Koike, S., Abe, S., Masaki, T. & Kaji, K. 2011. Effect of mast production on home range use of Japanese black bears. *The Journal of Wildlife Management*, 75, 867-875.

Krishnamani, R. 1994. Diet composition of the bonnet macaque (*Macaca radiata*) in a tropical dry evergreen forest of Southern India *Tropical Biodiversity*, 2, 285-302.

Kumar, R. S., Mishra, C. & Sinha, A. 2007. Foraging ecology and time-activity budget of the Arunachal macaque *Macaca munzala* – A preliminary study. *Current Science*, 93, 532-539.

Kunz, B. K. 2008. Frugivory and seed dispersal: ecological interactions between baboons, plants, and dung beetles in the savanna-forest mosaic of West Africa. PhD, University of Würzburg.

Kunz, B. K. & Linsenmair, K. E. 2008. Diet and behavioural ecology of olive baboons in the Comoé National Park. *Folia Primatologica*, 79, 31-51.

Kurland, J. A. 1973. A natural history of kra macaques (*Macaca fascicularis* Raffles, 1821) at the Kutai Reserve, Kalimantan Timur, Indonesia *Primates*, 14, 245-262.

Kurup, G. U. & Kumar, A. 1993. Time budget and activity patterns of the lion-tailed macaque (*Macaca silenus*). *International Journal of Primatology*, 14, 27-39.

Kwit, C., Levey, D. J. & Greenberg, C. H. 2004. Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. *Oikos*, 107, 303-308.

Lambert, J. E. 1998. Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evolutionary Anthropology*, 7, 8-20.

Lambert, J. E. 1999. Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *American Journal of Physical Anthropology*, 109, 365-386.

Lambert, J. E. 2001. Red-tailed guenons (*Cercopithecus ascanius*) and strychnos mitis: evidence for plant benefits beyond seed dispersal. *International Journal of Primatology*, 22, 189-201.

Lambert, J. E. 2002. Digestive retention times in forest guenons (*Cercopithecus* spp.) with reference to chimpanzees (*Pan troglodytes*). *International Journal of Primatology*, 23, 1169-1185.

Lambert, J. E. 2002. Exploring the link between animal frugivory and plant strategies: the case of primate fruit processing and post-dispersal seed fate. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 365-379. New York: CAB International.

Lambert, J. E. 2005. Competition, predation, and the evolutionary significance of the cercopithecine cheek pouch: the case of *Cercopithecus* and *Lophocebus*. *American Journal of Physical Anthropology*, 126, 183-192.

Lambert, J. E. 2010. Primate seed dispersers as umbrella species: a case study from Kibale National Park, Uganda, with implications for Afrotropical forest conservation. *American Journal of Primatology*, 71, 1-16.

Lambert, J. E. & Chapman, C. A. 2005. The fate of primate-dispersed seeds: deposition pattern, dispersal distance and implications for conservation. In: *Seed Fate - Predation, Dispersal and Seedling Establishment* (Ed. by Forget, P.-M., Lambert, J. E., Hulme, P. E. & Vander Wall, S. B.), pp. 137-150. Cambridge: CAB International.

Lambert, J. E. & Garber, P. A. 1998. Evolutionary and ecological implications of primate seed dispersal. *American Journal of Primatology*, 45, 9-28.

Lapenta, M. J. & Procópio-de-Oliveira, P. 2008. Some aspects of seed dispersal effectiveness of golden lion tamarins (*Leontopithecus rosalia*) in a Brazilian Atlantic forest. *Tropical Conservation Science*, 1, 122-139.

Laurance, W. F. 2005. The alteration of biotic interactions in fragmented tropical forests. In: *Biotic interactions in the tropics: their role in the maintenance of species diversity* (Ed. by Burslem, D. F. R. P., Pinard, M. A. & Hartley, S. E.). Cambridge Cambridge University Press.

Laurance, W. F. 2007. Forest destruction in tropical Asia. *Current Science*, 93, 1544-1550.

Laurance, W. F., Croes, B. M., Tchignoumba, L., Lahm, S. A., Alonso, A., Lee, M. E., Campbell, P. & Ondzeano, C. 2006. Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology*, 20, 1251-1261.

Lawes, M. J. 2002. Conservation of fragmented populations of *Cercopithecus mitis* in South Africa: the role of reintroduction, corridors and metapopulation ecology In: *The guenons: diversity and adaptation in African monkeys* (Ed. by Glenn, M. E. & Cords, M.), pp. 375-392. New York: Kluwer Academic/Plenum Publishers.

Lee, P. C. & Priston, N. E. C. 2005. Human attitudes to primates: perceptions of pests, conflict and consequences for primate conservation. In: *Commensalism and conflict: the human primate interface* (Ed. by Paterson, J. D. & Wallis, J.), pp. 1-23. Winnepeg: Hignell Printing.

Levey, D. J. & Byrne, M. M. 1993. Complex ant-plant interactions: rain-forest ants as secondary dispersers and post-dispersal seed predators. *Ecology*, 74, 1802-1812.

Levin, S. A., Muller-Landau, H. C., Nathan, R. & Chave, J. 2003. The ecology and evolution of seed dispersal: A theoretical perspective. *Annual Review of Ecology Evolution and Systematics*, 34, 575-604.

Li, D., Grueter, C. C., Ren, B., Zhou, Q., Peng, Z. & Wei, F. 2006. Characteristics of night-time sleeping places selected by golden monkeys (*Rhinopithecus bieti*) in the Samage forest, Baima Snow Mountain Nature Reserve, China. *Integrative Zoology*, 1, 141-152.

Li, H. & Zhang, Z. 2007. Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae). *Forest Ecology and Management*, 242, 511-517.

Lindburg, D. G. 1977. Feeding behaviour and diet of rhesus monkeys (*Macaca mulatta*) in a Siwalik forest in north India. In: *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes* (Ed. by Clutton-Brock, T. H.), pp. 223-249. London: Academic Press.

Liu, Z.-H. & Zhao, Q.-K. 2004. Sleeping sites of *Rhinopithecus bieti* at Mt. Fuhe, Yunnan. *Primates*, 45, 241-248.

LoGiudice, K. & Ostfeld, R. S. 2002. Interactions between mammals and trees: predation on mammal-dispersed seeds and the effect of ambient food. *Oecologia*, 130, 420-425.

Loiselle, B. A., Blendinger, P. G., Blake, J. G. & Ryder, T. B. 2007. Ecological redundancy in seed dispersal systems: a comparison between manakins (Aves: Pipridae) in two tropical forests. In: *Seed dispersal: theory and its application in a changing world* (Ed. by

Dennis, A. J., Schupp, E. W., Green, R. A. & Westcott, D. A.). Wallingford, UK: CAB International.

Lucas, P. W. & Corlett, R. T. 1991. Relationship between the diet of *Macaca fascicularis* and forest phenology. *Folia primatologica*, 57, 201-215.

Lucas, P. W. & Corlett, R. T. 1998. Seed dispersal by long-tailed macaques. *American Journal of Primatology*, 45, 29-44.

Lynam, A. J., Round, P. D. & Brockelman, W. Y. 2006. Status of birds and large mammals in Thailand's Dong Phayayen - Khao Yai forest complex. Wildlife Conservation Society.

MacKinnon, J. R. & MacKinnon, K. S. 1987. Conservation status of the primates of the Indo-Chinese subregion. *Primate Conservation*, 8, 187-195.

Maisels, F., Blake, S., Fay, M., Mobolambi, G. & Yako, V. 2006. A Note on the distribution of Allen’s swamp monkey, *Allenopithecus nigroviridis*, in northwestern Congo. *Primate Conservation*, 21, 93-95.

Makwana, S. C. 1978. Field ecology and behaviour of the rhesus macaque (*Macaca mulatta*): I. Group composition, home range, roosting sites, and foraging routes in the Asarori Forest. *Primates*, 19, 483-492.

Mangan, S. A., Schnitzer, S. A., Herre, E. A., Mack, K. M. L., Valencia, M. C., Sanchez, E. I. & Beve, J. D. 2010. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, 466, 752-756.

Marshall, A. J., Boyko, C. M., Feilen, K. L., Boyko, R. H. & Leighton, M. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. *American Journal of Physical Anthropology*, 140, 603-614.

Marshall, A. J. & Wrangham, R. W. 2007. Evolutionary consequences of fallback foods *International Journal of Primatology*, 28, 1219-1235.

Martin, R. D. 1990. A survey of living primates. In: *Primate Origins and Evolution. A phylogenetic reconstruction* (Ed. by Martin, R. D.), pp. 1-37. London: Chapman & Hall.

Martínez, I., García, D. & Obeso, J. R. 2008. Differential seed dispersal patterns generated by a common assemblage of vertebrate frugivores in three fleshy-fruited trees. *Ecoscience*, 15, 189-199.

Maruhashi, T. 1980. Feeding behavior and diet of the Japanese monkey (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, 21, 141-160.

Matsuda, I., Tuuga, A., Akiyama, Y. & Higashi, S. 2008. Selection of river crossing location and sleeping site by proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. *American Journal of Primatology*, 70, 1097-1101.

Matsuda, I., Tuuga, A. & Bernard, H. 2011. Riverine refuging by proboscis monkeys (*Nasalis larvatus*) and sympatric primates: Implications for adaptive benefits of the riverine habitat. *Mammalian Biology*, 76, 165-171.

McConkey, K. R. 2000. Primary seed shadow generated by gibbons in the rain forests of Barito Ulu, central Borneo. *American Journal of Primatology*, 52, 13-29.

McConkey, K. R. & Brockelman, W. Y. 2011. Non-redundancy in the dispersal network of a generalist tropical forest tree. *Ecology*, 92, 1492-1502.

McConkey, K. R. & Drake, D. R. 2006. Flying foxes cease to function as seed dispersers long before they become rare. *Ecology*, 87, 271-276.

McLoughlin, P. D. & Ferguson, S. H. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. *Ecoscience*, 7, 123-130.

Medellin, R. A. & Gaona, O. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica*, 31, 478-485.

Melnick, D. J. & Pearl, M. C. 1987. Cercopithecines in multimale groups: genetic diversity and population structure. In: *Primate Societies* (Ed. by Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T.), pp. 121-134. Chicago University of Chicago Press.

Melo, F. P. L., Martínez-Salas, E., Benítez-Malvido, J. & Ceballos, G. 2010. Forest fragmentation reduces recruitment of large-seeded tree species in a semi-deciduous tropical forest of southern Mexico. *Journal of Tropical Ecology*, 26, 35-43.

Ménard, N. 2004. Do echological factors explain variation in social organization? In: *Macaque societies: a model for the study of social organization* (Ed. by Thierry, B., Singh, M. & Kaumanns, W.), pp. 237-261. Cambridge: Cambrigde University Press.

Mendes Pontes, A. R. & 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.

Menon, S. & Poirier, F. E. 1996. Lion-tailed macaques (*Macaca silenus*) in a disturbed forest fragment: activity patterns and time budget. *International Journal of Primatology*, 17, 969-985.

Millennium Ecosystem Assessment. 2005. *Ecosystems and human well-being*. Washington, DC: Island Press.

Milton, K. 1980. *The foraging strategy of howler monkeys: A study in primate economics*. New York: Columbia University Press.

Milton, K. 2000. Quo vadis? Tactics of food search and group movement in primates and other animals. In: *On the move: How and why animals travel in groups* (Ed. by Boinski, S. & Garber, P. A.), pp. 375-417. Chicago and London: The University of Chicago press.

Milton, K. & May, M. L. 1976. Body weight, diet and home range area in primates. *Nature*, 259, 459-462.

Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. New York: John Wiley & Sons.

Muller-Landau, H. C. 2007. Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. *Biotropica*, 39, 372-284.

Murali, K. S. 1997. Patterns of seed size, germination and seed viability of tropical tree species in southern India. *Biotropica*, 29, 271-279.

Murray, P. 1975. The role of cheek pouches in cercopithecine monkey adaptative strategy. In: *Primate functional morphology and evolution* (Ed. by Tuttle, R. H.), pp. 151-194. The Hague: Mouton.

Muscarella, R. & Fleming, T. H. 2007. The role of frugivorous bats in tropical forest succession. *Biological Reviews*, 82, 573-590.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858.

Nahallage, C. A. D., Huffman, M. A., Kuruppu, N. & Weerasingha, T. 2008. Diurnal primates in Sri Lanka and people's perception of them. *Primate Conservation*, 23, 81-87.

Nakashima, Y., Lagan, P. & Kitayama, K. 2008. A study of fruit–frugivore interactions in two species of Durian (*Durio*, Bombacaceae) in Sabah, Malaysia. *Biotropica*, 40, 255-258.

Nakashima, Y. N. & Sukor, J. A. S. 2009. Importance of common palm civets (*Paradoxurus hermaphroditus*) as a long-distance disperser for large-seeded plants in degraded forests. *Tropics*, 18, 221-229.

Nathan, R. & Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, 15, 278-285.

National Research Council of the National Academies. 2003. *Nutrient Requirements of Nonhuman Primates*, Second revised edn. Washington, DC: The National Academies Press.

Naughton-Treves, L. 1998. Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conservation Biology*, 12, 156-168.

Naughton-Treves, L., Treves, A., Chapman, C. & Wrangham, R. 1998. Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, 35, 596-606.

Ngoprasert, D., Reed, D. H., Steinmetz, R. & Gale, G. A. in revision. Density estimation of Asian bears using chest mark based photographic capture-recapture sampling. *Ursus*.

Noma, N. & Yumoto, T. 1997. Fruiting phenology of animal-dispersed plants in response to winter migration of frugivores in a warm temperate forest on Yakushima Island, Japan. *Ecological Research*, 12, 119-129.

Nuñez-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, 348-354.

Oates, J. F. 1987. Food distribution and foraging behavior. In: *Primate Societies* (Ed. by Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T.), pp. 197-209. Chicago University of Chicago Press.

O'Brien, T. G. & Kinnaird, M. F. 1997. Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology*, 18, 321-351.

Oi, T. 1990. Population organization of wild pig-tailed macaques (*Macaca nemestrina nemestrina*) in West Sumatra. *Primates*, 31, 15-31.

Olupot, W., Chapman, C. A., Brown, C. H. & Waser, P. M. 1994. Mangabey (*Cercocebus albigena*) population density, group size, and ranging: a twenty-year comparison. *American Journal of Primatology*, 32, 197-205.

Olupot, W., Chapman, C. A., Waser, P. M. & Isabirye-Basuta, G. 1997. Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *American Journal of Primatology*, 43, 65-78.

Onderdonk, D. A. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *International Journal of Primatology*, 21, 587-611.

Ooi, M., Auld, T. & Whelan, R. 2004. Comparison of the cut and tetrazolium tests for assessing seed viability: a study using Australian native Leucopogon species. *Ecological management and restoration*, 5, 141-143.

Otani, T. 2004. Effects of macaque ingestion on seed destruction and germination of a fleshy-fruited tree, *Eurya emarginata*. *Ecological Research*, 19, 495-501.

Palmer, M. W. 1994. Variation in species richness: towards a unification of hypotheses. *Folia Geobotanica Phytotaxonomica*, 29, 511-530.

Pannell, J. R. 2007. Dispersal ecology: Where have all the seeds gone? *Current Biology*, 17, 360-362.

Parrotta, J. A. 2000. Catalysing natural forest restoration on degraded tropical landscapes. In: *Forest restoration for wildlife conservation* (Ed. by Elliott, S., Kerby, J., Blakesley, D., Hardwick, K., Woods, K. & Anusarnsunthorn, V.). Chiang Mai University, Thailand: International Tropical Timber Organisation and The Forest Restoration Research Unit.

Parrotta, J. A., Knowles, O. H. & Wunderle Jr, J. M. 1997. Development of floristic diversity in 10-years-old reforestation forests on a bauxite mined site in Amazonia. *Forest Ecology and Management*, 99, 21-42.

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L., Chini, L., Cooper, H. D., Gilman, E. L., Guénette, S., Hurtt, G. C., Huntington, H. P., Mace, G. M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R. J., Sumaila, U. R. & Walpole, M. 2010. Scenarios for global biodiversity in the 21st century. *Science*, 330, 1496-1501.

Peres, C. A. & van Roosmalen, M. 2002. Primate frugivory in two species-rich Neotropical forests: implications for the demography of large-seeded plants in overhunted areas. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.). New York: CAB International.

Phoonjampa, R., Koenig, A., Borries, C., Gale, G. A. & Savini, T. 2010. Selection of Sleeping Trees in Pileated Gibbons (*Hylobates pileatus*). *American Journal of Primatology*, 71, 1-9.

Pombo, A. R., Waltert, M., Mansjoer, S. S., Mardiastuti, A. & Mühlenberg, M. 2004. Home range, diet and behaviour of the Tonkean macaque (*Macaca tonkeana*) in Lore Lindu National Park, Sulawesi. In: *Land use, nature conservation and the stability of rainforest margins in southeast Asia* (Ed. by Gerold, G., Fremerey, M., Guhardja, E.), pp. 313-325. Berlin, Heidelberg: Springer.

Porter, L. M., Sterr, S. M. & Garber, P. A. 2007. Habitat use and ranging behavior of *Callimico goeldii*. *International Journal of Primatology*, 28, 1035-1058.

Poulsen, J. R., Clark, C. J., Connor, E. F. & Smith, T. B. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology*, 83, 228-240.

Poulsen, J. R., Clark, C. J. & Smith, T. B. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology*, 17, 787-808.

Pringle, E. G., Álvarez-Loayza, P. & Terborgh, J. 2007. Seed characteristics and susceptibility to pathogen attack in tree seeds of the Peruvian Amazon. *Plant Ecology*, 193, 211-222.

Priston, N. E. C. 2005. Crop-raiding by *Macaca Ochreata Brunnescens* in Sulawesi: reality, perceptions and outcomes for conservation, University of Cambridge

Rabinowitz, A. R. 1991. Behaviour and movements of sympatric civet species in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Journal of Zoology*, 223, 281-298.

Ramachandran, K. K. & Joseph, G. K. 2000. Habitat utilization of lion-tailed macaque (*Macaca silenus*) in Silent Valley National Park, Kerala, India. *Primate Report*, 58, 17-25.

Raemaekers, J. J. & Chivers, D. J. 1980. Socio-ecology of Malayan forest primates. In: *Malayan forest primates, ten years' study in tropical rain forest* (Ed. by Chivers, D. J.), pp. 279-316. New York: Plenum Press.

Raemakers, J. J., Aldrich-Blake, F. P. G. & Payne, J. F. 1980. The forest. In: *Malayan forest primates* (Ed. by Chivers, C. J.). New York: Plenum.

Ram, S., Venkatachalam, S. & Sinha, A. 2003. Changing social strategies of wild female bonnet macaques during natural foraging and on provisioning. *Current Science*, 84, 780-790.

Redford, K. H. & Feinsinger, P. 2001. The half-empty forest: sustainable use and the ecology of interactions. In: *Conservation of Exploited Species* (Ed. by Reynolds, J. D., Mace, G. M., Redford, K. H., Robinson, J. G., Gosling, M. L., Cowlishaw, G., Woodroffe, R. & Gittleman, J.), pp. 370-400. Cambridge: Cambridge University Press.

Reichard, U. 1998. Sleeping sites, sleeping places, and presleep behavior of gibbons (*Hylobates lar*). *American Journal of Primatology*, 46, 35-62.

Richard, A. F., Goldstein, S. J. & Dewar, R. E. 1989. Weed macaques: the evolutionary implications of macaque feeding ecology. *International Journal of Primatology*, 10, 569-594.

Ricklefs, R. E. 1990. *Ecology*, Third edn. New York: W. H. Freeman and Company.

Riley, E. P. 2007. Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. *International Journal of Primatology*, 28, 107-133.

Riley, E. P., Suryobroto, B. & Maestripieri, D. 2007. Distribution of *Macaca ochreata* and identification of mixed ochreata-tonkeana groups in South Sulawesi, Indonesia. *Primate Conservation*, 22, 129-133.

Righini, N., Serio-Silva, J. C., Rico-Gray, V. & Martínez-Mota, R. 2004. Effect of different primate species on germination of *Ficus* (*Urostigma*) seeds. *Zoo Biology*, 23, 273-278.

Robbins, M. M. & McNeilage, A. 2003. Home range and frugivory patterns of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology*, 24, 467-491.

Robertson, A. W., Trass, A., Ladley, J. J. & Kelly, D. 2006. Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. *Functional Ecology*, 20, 58-66.

Robinson, J. G. 1986. *Seasonal variation in use of time and space by the wedge-capped capuchin monkey,* Cebus olivaceus*: implications for foraging theory*. Washington: Smithsonian Institution Press.

Rodman, P. S. 1979. Skeletal differentiation of *Macaca fascicularis* and *Macaca nemestrina* in relation to arboreal and terrestrial quadrupedalism. *American Journal of Physical Anthropology*, 51, 51-62.

Rosenbaum, B., O'Brien, T. G., Kinnaird, M. & Supriatna, J. 1998. Population densities of Sulawesi crested black macaques (*Macaca nigra*) on Bacan and Sulawesi, Indonesia: effects of habitat disturbance and hunting. *American Journal of Primatology*, 44, 89-106.

Rowe, N. & Myers, M. 2011. All the World's Primates. www.alltheworldsprimates.org. Primate Conservation Inc. Charlestown RI. Downloaded on 10/10/2011. Charlestown RI.

Russo, S. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia*, 136, 80-87.

Russo, S. E. & Augspurger, C. K. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters*, 7, 1058-1067.

Russo, S. E., Portnoy, S. & Augspurger, C. K. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology*, 87, 3160-3174.

Saj, T., Sicotte, P. & Paterson, J. D. 1999. Influence of human food consumption on the time budget of vervets. *International Journal of Primatology*, 20, 977-994.

Saj, T., Sicotte, P. & Paterson, J. D. 2001. The conflict between vervet monkeys and farmers at the forest edge in Entebbe, Uganda. *African Journal of Ecology*, 39, 195-199.

Samuels, I. A. & Levey, D. J. 2005. Effects of gut passage on seed germination: do experiments answer the questions they ask? *Functional Ecology*, 19, 365-368.

Sargis, E. J., Terranova, C. J. & Gebo, D. L. 2008. Evolutionary morphology of the guenon postcranium and its taxonomic implications. In: *Mammalian evolutionary morphology:*

A tribute to Frederick S. Szalay (Ed. by Sargis, E. J.), pp. 361-372. New York: Springer-Verlag New York Inc.

Savini, T. 2005. Socioecology and reproduction in white-handed gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand. PhD thesis, Université de Liège.

Savini, T., Boesch, C. & Reichard, U. H. 2008. Home-range characteristics and the influence of seasonality on female reproduction in white-handed gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand. *American Journal of Physical Anthropology*, 135, 1-12.

Savini, T. & Kanwatanakid-Savini, C. 2011. Feeding overlap and seed dispersal efficiency between sympatric hornbills and gibbons in Thailand. *The Raffles Bulletin of Zoology*, 24, 115-122.

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J. & Gitzen, R. A. 1999. Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management*, 63, 739-747.

Seaman, D. E. & Powell, R. A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77, 2075-2085.

Schülke, O., Pesek, D., Whitman, B. J. & Ostner, J. 2011. Ecology of Assamese macaques (*Macaca assamensis*) at Phu Khieo Wildlife Sanctuary, Thailand. *Journal of Wildlife in Thailand*, 18.

Schupp, E. W. 1988. Factor affecting post-dispersal seed survival in a tropical forest. *Oecologia*, 76, 525-530.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*, 107/108, 15-29.

Schupp, E. W. 2007. The suitability of a site for seed dispersal is context-dependent. In: *Seed dispersal: Theory and its application in a changing world* (Ed. by Dennis, A. J., Schupp, E. W., Green, R. A. & Westcott, D.). Wallingford, UK: CAB International Publishing.

Schupp, E. W., Jordano, P. & Gómez, J. M. 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist*, 188, 333-353.

Schupp, E. W., Milleron, T. & Russo, S. 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. In: *Seed-dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 19-33. New York: CAB International.

Scott, R., Pattanakaew, P., Maxwell, J. F., Elliott, S. & Gale, G. 2000. The effect of artificial perches and local vegetation on bird-dispersed seed deposition into regenerating sites.

In: *Forest restoration for wildlife conservation* (Ed. by Elliott, S., Kerby, J., Blakesley, D., Hardwick, K., Woods, K. & Anusarnsunthorn, V.), pp. 326-337. Chiang Mai University, Thailand: International Tropical Timber Organisation and The Forest Restoration Research Unit.

Setchell, J. M. & Curtis, D. J. 2003. *Field and laboratory methods in primatology: practical guide*. Cambridge: Cambridge University Press.

Shah, N. F. 2003. Foraging strategies in two sympatric mangabey species (*Cercocebus agilis* and *Lophocebus albigena*). PhD, Stony Brook University.

Sillero-Zubiri, C. & Switzer, D. 2001. *Crop raiding primates: Searching for alternative, humane ways to resolve conflict with farmers in Africa*: People and Wildlife Initiative. Wildlife Conservation Research Unit, Oxford University.

Singh, M., Singh, M., Kumar, M. A., Kumara, H. N., Sharma, A. K. & Kaumanns, W. 2002. Distribution, population structure, and conservation of lion-tailed macaques (*Macaca silenus*) in the Anaimalai Hills, Western Ghats, India. *American Journal of Primatology,* 57, 91-102.

Singh, M. & Vinathe, S. 1990. Inter-population differences in the time budgets of bonnet monkeys (*Macaca radiata*). *Primates,* 31, 589-596.

Sinha, A. 2001. The bonnet macaque revisited: ecology, demography and behaviour. *ENVIS Bulletin: Wildlife and Protected Areas,* 1, 30-39.

Smith, A. C., Knogge, C., Huck, M., Löttker, P., Buchanan-Smith, H. M. & Heymann, E. W. 2007. Long-term patterns of sleeping site use in wild saddleback (*Saguinus fuscicollis*) and mustached tamarins (*S. mystax*): effects of foraging, thermoregulation, predation, and resource defense constraints. *American Journal of Physical Anthropology,* 134, 340-353.

Smith, L. W., Link, A. & Cords, M. 2008. Cheek pouch use, predation risk, and feeding competition in blue monkeys (*Cercopithecus mitis stuhlmanni*). *American Journal of Physical Anthropology,* 137, 334-341.

Sodhi, N. S., Koh, L. P., Brook, B. W. & Ng, P. K. L. 2004. Southeast Asian biodiversity: an impending disaster. *Trends in Ecology and Evolution,* 19, 654-660.

Son, V. D. 2003. Diet of *Macaca fascicularis* in a mangrove forest, Vietnam. *Laboratory Primate Newsletter,* 42, 1-5.

Spiegel, O. & Nathan, R. 2007. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters,* 10, 718-728.

Sponsel, L. E., Ruttanadakul, N. & Natadecha-Sponsel, P. 2002. Monkey business? The conservation implications of macaque ethnoprimatology in southern Thailand. In: *Primates face-to-face: Conservation implications of human-nonhuman primate interconnections* (Ed. by Fuentes, A. & Wolfe, L. D.), pp. 288-309. New York: Cambridge University Press.

Srivastava, A. 2006. Conservation of threatened primates of Northeast India. *Primate Conservation*, 20, 107-113.

Stevens, J. R., Rosati, A. G., Ross, K. R. & Hauser, M. D. 2005. Will travel for food: spatial discounting in two new world monkeys. *Current Biology*, 15, 1855-1860.

Stoner, K. E. & Henry, M. 2008. Seed dispersal and frugivory in tropical ecosystems. In: *Encyclopedia of Life Support Systems*. Oxford: Eolss Publishers.

Struhsaker, T. T. 1975. *The red colobus monkey*. Chicago: University of Chicago Press.

Strum, S. C. 2010. The development of primate raiding: implications for management and conservation. *International Journal of Primatology*, 31, 133-156.

Su, H.-H. & Lee, L.-L. 2001. Food habits of formosan rock macaques (*Macaca cyclopis*) in Jentse, Northeastern Taiwan, assessed by fecal analysis and behavioral observation. *International Journal of Primatology*, 22.

Sugardjito, J. 1983. Selecting nest-sites of Sumatran orangutans, *Pongo pygmaeus abelii* in the Gunung Leuser National Park, Indonesia. *Primates*, 24, 467-474.

Sukumar, R. 2006. A brief review of the status, distribution and biology of wild Asian elephants *Elephas maximus*. *International Zoo Yearbook*, 40, 1-8.

Suzuki, S., Kitamura, S., Kon, M., Poonswad, P., Chuailua, P., Plongmai, K., Yumoto, T., Noma, N., Maruhashi, T. & Wohandee, P. 2006. Foraging activity patterns of frugivorous or omnivorous animals on the forest floor of a tropical seasonal forest in Thailand, with reference to seasonal changes. *Natural History Bulletin of the Siam Society*, 54, 177-194.

Swedell, L. 2002. Ranging behavior, group size and behavioral flexibility in Ethiopian hamadryas baboons (*Papio hamadryas hamadryas*). *Folia primatologica*, 73, 95-103.

Tang, Z.-H., Cao, M., Sheng, L.-X., Ma, X.-F., Walsh, A. & Zhang, S.-Y. 2008. Seed dispersal of *Morus macroura* (Moraceae) by two frugivorous bats in Xishuangbanna, SW China. *Biotropica*, 40, 127-131.

Tenaza, R. R. & Tilson, R. L. 1985. Human predation and Kloss's gibbon (*Hylobates klossii*) sleeping trees in Siberut Island, Indonesia. *American Journal of Primatology*, 8, 299-308.

Terborgh, J., Nuñez-Iturri, G., Pitman, N. C. A., Cornejo Valverde, F. H., Alvarez, P., Swamy, V., Pringle, E. G. & Paine, C. E. T. 2008. Tree recruitment in an empty forest. *Ecology*, 89, 1757-1768.

Thierry, B., Singh, M. & Kaumanns, W. 2004. Why macaque societies? In: *Macaque societies: a model for the study of social organization* (Ed. by Thierry, B., Singh, M. & Kaumanns, W.), pp. 3-10. New York: Cambridge University Press.

Thomas, S. C. 1991. Population densities and patterns of habitat use among anthropoid primates of the Ituri Forest, Zaire. *Biotropica*, 23, 68-83.

Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics*, 1/2, 151-190.

Traveset, A., Riera, N. & Mas, R. E. 2001. Passage through bird guts causes interspecific differences in seed germination characteristics. *Functional Ecology*, 15, 669-675.

Traveset, A. & Verdú, M. 2002. A meta-analysis of the effect of gut treatment on seed germination. In: *Seed dispersal and frugivory: ecology, evolution and conservation* (Ed. by Levey, D. J., Silva, W. R. & Galetti, M.), pp. 339-350. New York: CAB International.

Tsuji, Y. 2010. Effects of the physical characteristics of seeds on gastrointestinal passage time in captive Japanese macaques. *Journal of Zoology*, 280, 171-176.

Tsujino, R. & Yumoto, T. 2009. Topography-specific seed dispersal by Japanese macaques in a lowland forest on Yakushima Island, Japan. *Journal of Animal Ecology*, 78, 119-125.

Tutin, C. E. G., Ham, R. M., White, L. J. T. & Harrison, M. J. S. 1997a. The primate community of the Lopé reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology*, 42, 1-24.

Tutin, C. E. G., White, L. J. T. & Mackanga-Missandzou, A. 1997b. The use by rain forest mammals of natural forest fragments in an Equatorial African savanna. *Conservation Biology*, 11, 1190-1203.

Twinomugisha, D. & Chapman, C. A. 2007. Golden monkey ranging in relation to spatial and temporal variation in food availability. *African Journal of Ecology*, 46, 585-593.

Twinomugisha, D., Chapman, C. A., Lawes, M. J., O'Driscoll Worman, C. & Danish, L. M. 2006. How does the golden monkey of the Virungas cope in a fruit scarce environment? In: *Primates of Western Uganda* (Ed. by Newton-Fisher, N. E., Notman, H., Reynolds, V. & Paterson, J. D.), pp. 45-60. New York: Springer.

Umapathy, G. & Kumar, A. 2000. Impacts of the habitat fragmentation on time budget and feeding ecology of lion-tailed macaque (*Macaca silenus*) in rain forest fragments of Anamalai Hills, South India. *Primate Report*, 58, 67-82.

Valenta, K. & Fedigan, L. M. 2008. How much is a lot? Seed dispersal by white-faced capuchins and implications for disperser-based studies of seed dispersal systems. *Primates*.

Valenta, K. & Fedigan, L. M. 2009. Effects of gut passage, feces, and seed handling on latency and rate of germination in seeds consumed by capuchins (*Cebus capucinus*). *American Journal of Physical Anthropology*, 138, 486-492.

Vanthomme, H., Bellé, B. & Forget, P. M. 2010. Bushmeat hunting alters recruitment of large-seeded plant species in Central Africa. *Biotropica*, 42, 672-679.

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.

Verdú, M. & Traveset, A. 2005. Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. *Ecology*, 86, 1385-1394.

Vessey, S. H. 1973. Night observations of free-ranging rhesus monkeys. *American Journal of Physical Anthropology*, 38, 613-620.

von Hippel, F. A. 1998. Use of sleeping trees by black and white colobus monkeys (*Colobus guereza*) in the Kakamega. *American Journal of Primatology*, 45, 281-290.

Vulinec, K., Lambert, J. E. & Mellow, D. J. 2006. Primate and dung beetle communities in secondary growth rain forests: implications for conservation of seed dispersal systems. *International Journal of Primatology*, 27, 855-879.

Warren, Y. 2008. Crop-raiding baboons (*Papio anubis*) and defensive farmers: a West African perspective. *West African Journal of Applied Ecology*, 14, 1-11.

Weir, J. E. S. & Corlett, R. T. 2007. How far do birds disperse seeds in the degraded tropical landscape of Hong Kong, China? *Landscape Ecology*, 22, 131-140.

Wenny, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monographs*, 70, 331-351.

Wenny, D. G. 2001. Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evolutionary Ecology Research*, 3, 51-74.

Weyher, A. H., Ross, C. & Semple, S. 2006. Gastrointestinal parasites in crop raiding and wild foraging *Papio anubis* in Nigeria. *International Journal of Primatology*, 27, 1519-1534.

Wheatley, B. P. 1980. Feeding and ranging of East Bornean *Macaca fascicularis*. In: *The macaques: studies in ecology, behavior and evolution* (Ed. by Lindburg, D. G.), pp. 215-246. New York: Van Nostrand Reinhold Company.

Whitaker, D. M., Stauffer, D. F., Norman, G. W., Devers, P. K., Edwards, J., Giuliano, W. M., Harper, C., Igo, W., Sole, J., Spiker, H. & Tefft, B. 2007. Factors associated with variation in home-range size of Appalachian Ruffed Grouse (*Bonasa umbellus*). *The Auk*, 124, 1407-1424.

Whitington, C. 1990. Seed dispersal by white-handed gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand. MSc thesis, Mahidol University.

Whitington, C. L. 1992. Interactions between lar gibbons and pig-tailed macaques at fruit sources. *American Journal of Primatology*, 26, 61-64.

Wieczkowski, J. 2005. Comprehensive conservation profile of Tana mangabeys. *International Journal of Primatology*, 26, 651-660.

Willson, M. & Traveset, A. 2000. The ecology of seed dispersal. In: *Seeds: the ecology of regeneration in plant communities* (Ed. by Fenner, M.), pp. 85-110. Wallingford, UK: CAB International.

Wilson, D. E. & Reeder, D. M. 2005. *Mammal species of the world. A taxonomic and geographic reference*, 3rd edition edn: Johns Hopkins University Press.

Woodroffe, R., Thirgood, S. & Rabinowitz, A. 2005. The impact of human-wildlife conflict on natural systems. In: *People and wildlife: conflict or coexistence?* (Ed. by Woodroffe, R., Thirgood, S. & Rabinowitz, A.). Cambridge: Cambridge University Press.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70, 164-168.

Wrangham, R. W., Chapman, C. A. & Chapman, L. J. 1994. Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology*, 10, 355-368.

Wrangham, R. W., Conklin-Brittain, N. L. & Hunt, K. D. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology*, 19, 949-970.

Wrangham, R. W., Gittleman, J. L. & Chapman, C. A. 1993. Constraints on group size in primates and carnivores: population density and day-range as assays of expoitation competition. *Behavioral Ecology and Sociobiology*, 32, 199-209.

Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, 130, 1-14.

Wright, S. J. 2005. Tropical forests in a changing environment. *Trends in Ecology & Evolution*, 20, 553-560.

Wright, S. J. & Duber, H. C. 2001. Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica*, 33, 583-595.

Wright, S. J., Hernandéz, A. & Condit, R. 2007. The bushmeat harvest alters seedling banks by favoring lianas, large seeds, and seeds dispersed by bats, birds, and wind. *Biotropica*, 39, 363-371.

Wright, S. J. & Muller-Landau, H. C. 2006. The future of tropical forest species. *Biotropica*, 38, 287-301.

Wright, S. J., Stoner, K. E., Beckman, N., Corlett, R. T., Dirzo, R., Muller-Landau, H. C., Nuñez-Iturri, G., Peres, C. A. & Wang, B. C. 2007. The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica*, 39, 289-291.

Wright, S. J., Zeballos, H., Domínguez, I., Gallardo, M. M., Moreno, M. C. & Ibáñez, R. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology*, 14, 227-239.

Wunderle, J. M. J. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forestry Ecology and Management*, 99, 223-235.

Yumoto, T., Noma, N. & Maruhashi, T. 1998. Cheek-pouch dispersal of seeds by Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, 39, 325-338.

Zabel, C. J., McKelvey, K. & James P. Ward, J. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). *Canadian Journal of Zoology*, 73, 433-439.

Zhang, S.-Y. 1995. Sleeping habits of brown capuchin monkeys (*Cebus apella*) in French Guiana. *American Journal of Primatology*, 36, 327-335.

Zhao, Q.-K. 1999. Responses to seasonal changes in nutrient quality and patchiness of food in a multigroup community of Tibetan macaques at Mt. Emei. *International Journal of Primatology*, 20, 511-524.