Aus dem

Leibniz-Institut für Zoo- und Wildtierforschung (IZW)

Im Forschungsverbund Berlin e.V.

eingereicht beim

Fachbereich Veterinärmedizin

Professur für interdisziplinäre Zoo- und Wildtierkunde

Freie Universität Berlin

The conservation management and conservation medicine of orang-utan (*Pongo pygmaeus morio*) in Sabah, Malaysia

Inaugural-Dissertation

zur Erlangung des Grades eines

Doktors der Veterinärmedizin

an der

Freien Universität Berlin

vorgelegt von

Marc Ancrenaz

Tierarzt aus Antony (Frankreich)

Berlin 2015

Journal-Nr.: 3772

Gedruckt mit Genehmigung des Fachbereichs Veterinärmedizin
der Freien Universität Berlin

Dekan:	Univ.-Prof. Dr. Jürgen Zentek
Erster Gutachter:	Univ.-Prof. Dr. Heribert Hofer
Zweiter Gutachter:	Prof. Dr. Carsten Niemitz
Dritter Gutachter:	Univ.-Prof. Dr. Christa Thöne-Reineke

Deskriptoren (nach CAB-Thesaurus):
Behavior, activity, oil palm, plantations, population ecology, population structure, conservation, animal health, public health, ecotourism, travel medicine, Pongidae, Hominidae, Malaysia

Tag der Promotion: 13.04.2015

Bibliografische Information der *Deutschen Nationalbibliothek*
Die Deutsche Nationalbibliothek verzeichnet diese Publikation in der Deutschen Nationalbibliografie; detaillierte bibliografische Daten sind im Internet über <http://dnb.ddb.de> abrufbar.

ISBN: 978-3-86387-605-0
Zugl.: Berlin, Freie Univ., Diss., 2015
Dissertation, Freie Universität Berlin
D 188

Choriner Str. 85 - 10119 Berlin
verlag@menschundbuch.de – www.menschundbuch.de

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CHAPTER 1: GENERAL INTRODUCTION

1. The biodiversity crisis in South East Asia: extent of the issue

The human component

Owing to the high number of species of endemic plants and animals, South East Asia (Brunei Darussalam, Cambodia, Indonesia, Lao PDR, Malaysia, Myanmar, the Philippines, Singapore, Thailand and Vietnam) is one of the major biodiversity hotspots in the world (Myers *et al*., 2000). However, South East Asia also contains the highest proportion of endangered taxa for vascular plants, birds and mammals in the world, making this biodiversity hotspot one of the top priority areas for conservation worldwide (Sodhi *et al*., 2010; Duckworth *et al*., 2012). Although extremely complex in its details, the crisis faced by biodiversity in South East Asia is primarily the consequence of exponential human growth and the subsequent exploitation of natural ecosystems to fulfill the growing needs of the human population. The ten countries of South East Asia listed above represent 3.0% of the planet's land mass but are occupied by 8.9% of the world human population. In the region, human population density increases at a yearly rate of about 1.5% (UNSD, 2012). In addition, approximately 40% of the world's human population lives in three of the countries surrounding South East Asia (China, India, Bangladesh), in an area representing only 8.8% of the planet's land mass.

Agriculture expansion and other threats

In South East Asia, human density is negatively associated with forest cover and positively with the number of threatened species (Sodhi *et al*., 2010), and annual deforestation rates are the highest among all tropical countries. This rate has increased regularly over the past two decades (Sodhi *et al*., 2010). Forests are used for timber extraction, and until recently timber exports from Borneo alone were higher than all of tropical Africa and Latin America combined (Cleary *et al*., 2007). Forest loss in the region primarily results from conversion to agriculture: slash-and-burn practices for subsistence by smallholders, and agro-industrial monoculture for introduced species such as oil palm *Elaeis guineensis*, rubber *Hevea brasiliensis*, *Acacia* and *Eucalyptus*. For example, more than 55% of oil palm development that occurred in Malaysia and Indonesia between 1990 and 2005 replaced intact and logged-over forests, (i.e. forests that have been heavily exploited and have lost most of their timber resources) (Koh & Wilcove, 2008). In most places, agricultural ecosystems are becoming the dominant landscape, just as they have, for centuries, dominated temperate regions.

Compared to intact forests, the structure and composition of over-exploited forests and agriculture landscapes are overly simplified. Tree density, diversity, and tree canopy layers are reduced (in extreme cases, such as development of paddy fields or annual crops, these canopy layers are completely removed). Top soil is stripped by erosion or damaged by compaction, and microclimate conditions often become drier and hotter. Consequently, these new conditions bring changes in wildlife community structure and abundance, with endemic and specialized taxa most at risk of being replaced with invasive and generalist taxa (Meijjard *et al*., 2005).

Throughout the tropics, these negative impacts are compounded by the overharvesting of forest products and unsustainable rates of hunting (Sodhi *et al*., 2010). The quantity of fossils and remains found in South East Asia show that hunting is not a new threat to wildlife (Rijksen & Meijaard, 1999). However, demands for wildlife and wildlife parts are fuelled with economic growth, easier access to natural habitats through improved infrastructures (roads) and vehicles, and more effective and easily available weapons (rifles, snares). Consequently, many wildlife species have been decimated during the last decades to supply local and regional markets with meat, antlers, horns and other body parts for bush meat, pet or traditional medicine trades (Steinmetz *et al*., 2010; Duckworth *et al*., 2012). In the worst cases, overhunting practices have resulted in the “empty forest syndrome” (Robinson & Benneth, 2000; Corlett, 2007).

The general health of wildlife populations surviving in or successfully adjusting to these fractured landscapes is further affected by additional threats such as pollution, emerging diseases, hybridization with domestic livestock for some wildlife species, and human-wildlife conflicts arising from the damage which some wildlife species such as carnivores, primates or elephants and etc. may inflict on cultivated areas or livestock. In turn, displaced wildlife populations become more sensitive to natural catastrophes such as floods or droughts, fires (natural or man-made) and climate change, genetic drift and inbreeding. All these causes lead to a global extinction crisis of unprecedented magnitude, with multifaceted consequences. The long-term impacts of these changes are still not fully understood: the relationship between wildlife diversity, abundance and distribution and forest regeneration (seed dispersal and germination), changes in trophic cascades – in particular predator-prey relationships and the worldwide removal of an entire trophic level (Estes *et al*., 2011), shifts of population distributions as a consequence of climate change, and emerging diseases. What is already known is that changes in the composition of wildlife communities affect the functionality of ecosystems and impoverish the value of the services which they provide.

In addition to their effects on wildlife populations, human communities are also negatively affected by the intense and rapid transformation of the environment. The destruction of natural resources used by rural communities (wildlife species and plants used as food, timber, and non-timber forest products) exacerbates the hardships already faced by the poorest human groups

(Martinez-Alier, 2003). In many areas, forest reduction and loss lead to the reduction or loss of a major source of protein (Benneth *et al*., 2000) or increased human-animal conflict for rural communities, who often have to bear the consequences of these conflicts (Woodroffe *et al*., 2005). As a consequence, environmental change and the resulting hardships culminate in mass migrations from rural to urban areas. The social ramifications of this have yet to be fully understood, as this move means the loss of natural heritage, tradition and culture valued by local communities (Meijaard *et al*., 2013; Ancrenaz and Lackman, 2014).

- **Maintaining elements of enhanced biodiversity in man-made landscapes**

More and more empirical evidence shows an unexpected resilience of biodiversity to human disturbance. Although primary forests are irreplaceable for some species of tropical forests, selectively logged forests are able to maintain a relatively high level of biodiversity (Gibson *et al*., 2011). The role of exploited forests for biodiversity conservation is still debated today (Zimmerman & Kormos, 2012) but many scientists are convinced that because of their ecological value, secondary and degraded forests are still worth protecting (Meijaard *et al*., 2005; Sheil & Meijaard, 2010). Similarly, even though croplands retain less diverse and abundant biodiversity than natural forests, these man-made landscapes can still harbor and accommodate a substantial number of species (Mendenhall *et al*., 2014). Well managed plantations can provide foraging resources and dispersal opportunities for various species (Maddox *et al*., 2011). Moreover, it is important to ensure that these agricultural landscapes can retain some functional ecological role to guarantee a certain level of ecosystem services (Foster *et al*., 2011). Resilience and adaptability are characteristic evolutionary traits to many ecosystems and wildlife species (Gunderson *et al*., 2010). These characteristics need to be better understood in order to be taken into consideration when designing alternative conservation strategies which aim to reconcile human development and the viability of wildlife communities (see Figure 1.2, page 15).

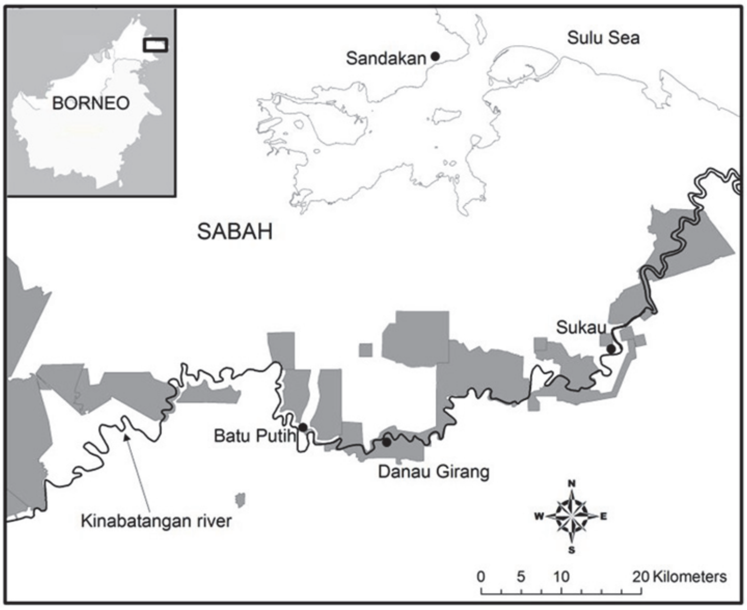


Figure 1.1: Map showing the location of the forests (grey areas) of lower Kinabatangan in East Sabah (Malaysian Borneo). The white areas are human-transformed landscapes (primarily extensive agro-industrial palm oil plantations).

This dissertation uses the results of scientific studies that I have conducted and supervised in Kinabatangan and in Sabah about the North East Bornean Orang-utan (*Pongo pygmaeus morio*) as an entry point to illustrate the new and complex situation faced by wildlife conservation in the deeply altered environment of Borneo's island (see Figure 1.1). It also discusses what could be done to improve the conservation status of the species. Great Apes are our closest living relatives (Harrison, 2010). Despite the appeal and strong iconic value of all great apes, decades of conservation efforts and significant financial resources committed to their preservation have globally failed to halt the decline of their populations (Caldecott & Miles, 2009). In this section, I highlight a few reasons that have contributed to this failure and how some of these issues have been addressed in Sabah (Figure 1.2, page 15).

2. Protecting orang-utans in Borneo: where are the major populations?

- **Challenges to survey orang-utans**

One of the prerequisites for effective species protection is a reliable knowledge regarding the distribution, density and size of the populations we intend to protect. This information is difficult to obtain for orang-utans because of a number of traits inherent to both species: shy, elusive and cryptic, and a low abundance throughout its range, making direct sightings a rare event (Blouch, 1997). Further difficulties result from the habitat characteristics where they are found: tropical forests offer limited visibility, are usually difficult to access and inhospitable in nature. As a result, early estimates in the 1960s and 1970s for Bornean orang-utan varied between a few thousands and 156,000 individuals, illustrating the difficulties to establish a baseline knowledge on population distribution and abundance (Schaller, 1961; Mac Kinnon, 1986). Conventionally, the estimation of great ape abundance is based on the number and the spatial distribution of their nests. This is usually obtained from ground nest surveys along line transects (Yoshiba, 1964; Ghiglieri 1984; Tutin & Fernandez, 1984; van Schaik *et al*., 1995; Kuehl *et al*., 2008). This approach is unrealistic to cover the entire 90,000 km^2 of the estimated orang-utan range in Borneo (Wich *et al*., 2012a).

- **New survey methodologies reveal that most orang-utan populations in Borneo are found outside protected areas**

To overcome the difficulties faced by traditional surveys conducted on the ground, I designed a new methodology to count orang-utan nests from a helicopter as part of the “Kinabatangan Orang-utan Conservation Programme” (KOCP) (Ancrenaz *et al*., 2005). Aerial nest counts allowed us to significantly increase the size of the sampling area, provided a way to survey remote areas not easily accessible from the ground, were considerably faster and were cheaper than classic ground surveys. The new aerial approach proved to be an efficient way to document the precise range of all orang-utan populations throughout the state of Sabah. It also gave the first reliable estimates of the population size at the state level: with a total of about 11,000 individuals (95% confidence interval: 8,317 – 18,376), the state of Sabah was the major stronghold in Borneo for the subspecies *Pongo pygmaeus morio* (Ancrenaz *et al*., 2005).

More importantly, these surveys revealed that in the early 2000s more than 60% of wild orang-utan populations were found outside protected areas in Sabah. Major populations were located in logged-over forests at different stages of exploitation, degradation and regeneration, and in man-made landscapes such as industrial tree plantations (acacia, palm oil, and others).

Although aerial surveys significantly increased our understanding of the status of the orang-utan in Sabah, replicating this methodology in the whole of Kalimantan, the largest area of Borneo which is part of the Republic of Indonesia, has been difficult: availability of helicopters or fixed-wing aircrafts is often limited, there are areas of great ape's range that are not accessible by small aircrafts and costs and safety issues may be prohibitive (Ancrenaz, 2007). New technologies, such as unmanned drones (small automated and computer-guided flying machines) could offer alternative solutions and assist conservationists to collect data in the field more easily (Koh & Wich, 2012).

The most recent technological advances in geography and spatial ecology, including the development of powerful geographic information systems software, iterative algorithms for modeling and simulation purposes, in satellite imagery and in remote sensing provide powerful tools that make landscape analysis more precise and efficient than in the past (Knight *et al.*, 2006). This also includes new techniques of predictive modeling, such as the maximum entropy (Maxent) approach, which integrate positive presence location data with key biological determinants and do not require the traditional sampling design for a study area where for each segment comprehensive presence/absence information is available. In combination, these powerful tools are highly useful to help identify landscapes or regions which could be suitable for a target species or locations currently occupied by a specific species (Elith *et al.*, 2006; Philips *et al.*, 2006; Franklin, 2009).

The data of the aerial surveys I led in Sabah were used for a remote sensing analysis throughout Borneo. The results of this exercise showed that in the early 2010s approximately 22% of the current Bornean orang-utan distribution was located in protected areas throughout the island, whereas the rest (or 78%) of the populations fall outside protected areas (Wich *et al.*, 2012a). Approximately a third of the entire orang-utan range is within commercial forest reserves that are exploited for timber, and about 45% falls within forest areas earmarked for conversion to agriculture or other land-uses. A business-as-usual scenario, according to which non-protected forests would be converted along the lines of current development plans, will result in the loss of more than half of the current orang-utan range on the island of Borneo. Under such a scenario, only a small percentage of the current orang-utan habitat in Borneo would be left undisturbed by infrastructure development by 2030 (Gaveau *et al.*, 2013).

3. Is there a future for orang-utans in commercial forest reserves?

The results of our aerial surveys in Sabah and of the Borneo-wide meta-analysis showed that a significant part of the current orang-utan range was found in forests exploited for timber. This result strongly emphasized the need to investigate the potential role of commercial forests exploited for timber in orang-utan conservation. Several questions needed to be investigated:

(1) Are orang-utan populations found in exploited forests viable or not?

(2) What are the ecological requirements necessary to sustain healthy populations in exploited forests?

(3) Is it possible to develop better management practices that reconcile economic exploitation of timber resources and orang-utan survival?

In order to improve our understanding of the potential value of logged forests for orang-utan conservation, I designed and supervised a series of surveys in Sabah targeting exploited forests in order to better understand how forest exploitation could impact orang-utan abundance.

Without any doubt, logging is harmful to many wildlife species, especially to forest specialists characterized by a narrow ecological niche and very specific requirements, and the negative impacts of logging are magnified by extraction intensity (Edwards *et al*., 2010). Originally, it was believed that orang-utans were extremely sensitive to forest degradation. The early generations of orang-utan researchers were convinced that forests exploited for timber would yield lower orang-utan densities than primary forests free of human influences (Rao and van Schaick, 1997), and that intense degradation following large-scale conventional logging would result in orang-utan decline and subsequent local extinction (Husson *et al*., 2009). The general feeling was that secondary forests were not valuable for orang-utan conservation (Riksen & Meijaard, 1999).

However, the negative impacts of the ecological changes following timber extraction were often confounded with hunting pressure that is usually associated with forest exploitation. Indeed, it is now well established that overall orang-utan distribution is better explained by land elevation and hunting pressure than by forest exploitation itself (Marshall *et al*., 2006; Wich *et al*., 2012b). Because orang-utans are very slow breeders, yearly off-takes higher than 1% will wipe out a population within decades, irrespective of its initial size (Marshall *et al*., 2009). Hunting is therefore seen as the major underlying factor and explanatory reason for orang-utan extinction in exploited forests (Meijaard *et al*., 2011a).

In order to better understand what would be the consequences of forest exploitation on orang-utan abundance and distribution, I supervised systematic aerial and ground surveys at a large scale in the logged and logged-over forests of several forest reserves in Sabah: Kinabatangan (Ancrenaz *et al*., 2004b), Deramakot, Ulu Segama and Malua Commercial Forest Reserves (Chapter 2), etc. These surveys showed that slightly logged forests could support relatively high orang-utan densities, sometimes higher than in neighboring mature primary forests (Danum Valley Conservation Area for example). They also indicated that orang-utan survival was strongly related to the geographic scale and to the intensity of logging activities. At the local scale, many animals tend to leave areas when they are exploited and disturbed by logging operations before moving back after exploitation is over. This re-colonization process strongly depends on the level of degradation and regeneration of the habitat (Chapter 2). Importantly, surveys conducted in Sabah showed that heavy rates of timber extraction resulted in extremely damaged habitats and in low to extremely low orang-utan densities in response to simplification of forest structure, heavy structural and incidental damages to all tree size-classes, and the destruction of fallback food sources (Johns, 1988). In the worst cases, heavy and unsustainable extraction rates conducted on a large geographic scale resulted in significant population decline, even in the absence of hunting (as in the case of North Ulu Segama).

4. Orang-utans in agro-industrial landscapes

The resilience of the orang-utan and its ability to cope with drastic habitat changes is further illustrated by recent records of species presence in acacia plantations in East Kalimantan (Meijaard *et al.*, 2010) and mature oil palm plantations in Sabah (Chapter 3). In Sumatra, stable groups of orang-utans have survived in a mosaic of mixed agriculture and forest for over 20 years (Campbell-Smith *et al.*, 2011a). The behavioral and feeding ecology of orang-utans who survive in these man-made landscapes differ markedly from what is known in primary forest, including smaller home ranges and travelled distances, increased terrestriality, less time spent foraging, predominantly cultivated fruit diet, increased tolerance to close human proximity (Campbell-Smith *et al.*, 2011b; Chapter 3). These changes further reinforce the idea that to a certain extent orang-utans are flexible enough to substantial changes in their natural environment. Although agro-industrial plantations alone cannot sustain viable populations, orang-utans utilize areas of monoculture for dispersal and travel through plantations to move from one isolated patch of forest to another (Meijaard *et al.*, 2010; Campbell-Smith *et al.*, 2012; Chapter 3). They feed on acacia bark and the fronds and fruits of oil palm. They also use both acacia and palms to build their nests. However, it is still unclear whether the orang-utans found in these agro-industrial plantations are part of resident sub-populations in a local re-colonization stage or whether they are transient and dispersing individuals that would be part of a much larger population encompassing a wider range.

In the latest survey of orang-utan distribution within the oil palm plantations of Kinabatangan in Eastern Sabah, we showed that more than 90% of the signs indicating orang-utan presence (nests, broken leaves) were found less than 50 m away from small forest patches or forest edges. These findings suggest that orang-utans extensively use patches of forests and non-palm trees in this landscape and that the penetration of homogenous stands of oil palms is relatively weak unless non-palm trees are present. However, signs of orang-utans (broken leaves) were also recorded more than 500 m from a forest, indicating that orang-utans can sometimes venture further from a forest edge into an oil palm plantation (Chapter 3). Through precise mapping of the industrial landscape of the Kinabatangan we were able to determine that some orang-utans could cross up to 4 km of pure mature oil palm stands in order to move between isolated forest patches (Chapter 3).

5. Unsuspected terrestrial behavior

Over the past several decades orang-utan research has generated a significant amount of scientific literature, resulting in what people generally think is an appropriate knowledge about the ecology and biology of the species (see Wich *et al.*, 2009 for a review). However, recent technology and the creation of innovative tools can bring new information and substantially challenge the knowledge we have of a species such as the orang-utan. For example, camera traps are a tool that gains momentum to study and to monitor wildlife populations in the tropics, particularly in habitats difficult to access. This tool also has the invaluable advantage of working independently of an observer once they have been set up (Ancrenaz *et al.*, 2012). Camera traps can detect intimate behaviors that are seldom observed by researchers during direct follows of the target species, they can provide data about activity patterns or allow for some abundance estimates in certain cases (O'Connel *et al.*, 2011). Not surprisingly, camera traps have been recently used to study terrestrial vertebrates at many different sites throughout Borneo. I therefore decided to initiate a meta-analysis of tens of thousands of pictures that had been taken during these studies to investigate orang-utan activity pattern and terrestrial behavior.

Orang-utans are the largest arboreal primates and possess several postcranial traits particularly adapted for the complex and dynamic arboreal environment (Rijksen & Meijaard, 1999; Delgado & van Schaik, 2000). Both species are indeed the largest arboreal mammal in the world (Cant 1987; Thorpe & Crompton, 2007). Although the presence of these adaptations suggests that ground locomotion should be an exception, ground locomotion has been occasionally reported from several areas in Borneo, particularly in large adult males (Mac Kinnon, 1974; Galdikas, 1979; Rodman, 1979; Tutlle, 1986). It is commonly assumed that habitat disturbance would force the arboreal orang-utan to come to the ground more frequently and thereby disrupt its natural behavior, as already mentioned in 1869 by Wallace:

> "*… a wide extent of unbroken and equally lofty virgin forest is necessary to the comfortable existence of these animals. Such forests form their open country, where they can roam in every direction […], passing from tree-top to tree-top without ever being obliged to descend upon the earth. The elevated and drier districts are more frequented by man, more cut up clearings and low second-growth jungle—not adapted to its peculiar mode of progression, and where it would therefore be more exposed to danger and more frequently obliged to descend upon the earth.*"

Increased terrestriality could increase the risk of predation, interactions with and persecution by people and exposure to novel pathogens. Yet, until now, very little scientific knowledge has been available about orang-utan terrestriality (but see Loken *et al*., 2013) and whether and how this species might cope with the intense transformation of its natural habitat (Mac Kinnon, 1974).

With a team of scientists who worked throughout Borneo, I led a large-scale species-level analysis of orang-utan terrestriality based on a comprehensive camera trapping data set from 16 sites across Borneo that was recently conducted to further investigate this behavior (Chapter 4).

The results of this analysis established that orang-utan terrestriality occurs at similar rates in primary mature growth and heavily degraded forests. Surprisingly, the rate was lower in selectively logged areas, likely because of the higher number of climbing opportunities (Chapter 4). We also showed that all sex-age classes are captured by camera-traps walking on the ground: large flanged males, as well as small males and females with and without offspring, suggesting that terrestriality is part of the species' natural behavior. Last but not least, this analysis across many study sites, habitats and landscapes also established that orang-utan terrestriality is influenced by forest structure, the animals being more frequently photographed under large canopy gaps than anywhere else.

The aspects of orang-utan terrestriality documented in this study reinforce the idea that new tools and technology can bring new information to the existing knowledge we have on a species. The fact that orang-utan can move on the ground more than expected may indicate that this species is more resilient and tolerant to drastic habitat changes than previously thought.

All these findings have implications for both research and conservation of one of our closest relatives, with strong repercussions for strategic conservation planning for the range countries of the orang-utan.

6. Risks of sanitary exposure to pathogen agents in multiple-use landscapes

Anthropozoonotic infection, or disease transmission between vertebrate species to and from people, can result from direct contact between people and animals, aerosolization of pathogens or contamination through feces and other biological discharges (Brack, 1987; Woodford *et al*., 2002). Infectious diseases are increasingly perceived as one of the greatest risks to the survival of great apes in the wild (Aguirre *et al*., 2002). Conservation medicine is especially relevant in areas where people and great apes come in close contact, as is the case of human-transformed landscapes or when great apes are used for eco-tourism activities (Boesh, 2008; Kongden *et al*., 2008; Walsh *et al*., 2003: Ryan & Walsh, 2011).

- **Intestinal infestation of wild orang-utans living in human-made landscapes**

Increased terrestrial locomotion in human-occupied landscapes (such as forests exploited by people or multiple-use forests) could in theory expose orang-utans to a greater risk of contamination with pathogens from human origin. The Kinabatangan floodplain is a perfect study area to evaluate this risk: a significant number of orang-utans still survive in highly degraded and fragmented forests that are heavily used by people (Ancrenaz *et al*., 2004b; Ancrenaz *et al*., 2005). I decided to investigate whether this situation could have significant consequences for the sanitary status of the resident orang-utan population found at the intensive study site established by KOCP in 1998. In order to compare the presence of gastro-intestinal parasites in wild orang-utans subjected to different intensities of human contact, we collected 23 fecal samples from 22 wild, unhabituated orang-utans (individuals that are not regularly in contact with people), 80 fecal samples from five wild, habituated orang-utans used for tourism activities (regular contact), and 31 samples from 31 captive individuals being rehabilitated and living at Sepilok rehabilitation center (unpublished results, 2010). For each sample, parasite identification and quantification was conducted with the ethyl acetate sedimentation technique (Muehlenbein, 2005).

Overall, parasites were detected in 72% of fecal samples collected on wild orang-utans. In average, positive samples were infested with 2.5 different types of parasites. The commonest parasites were eggs of hookworms (nematodes from the family Strongylidae, including *Ancylostoma* sp., *Necator* sp., *Angiostrongylus* sp., *Metastrongylus* sp.) etc., with 39% of positive samples, followed by *Balantidium coli* (30.4%), *Entamoeba coli* (29.7%), *E. histolytica* and larvae of *Strongyloides* sp. (Rhabditida, 18.3%), *E. nana* (10.9%), *Iodamoeba* sp. and *Trichuris sp.* (Adenophorea, 7.3%), larvae of *Trichostrongyloidea sp*. (6.1%). Parasites such as *Giardia* sp., *Ascaris* sp., *Enteroebius vermicularis* and possibly *Baylisascaris procyonis* were identified only once in our set of samples. All these parasites have already been documented in Bornean orang-utans except for *Enteroebius vermicularis* and *Baylisascaris procyonis* (Foitova *et al*., 2009). Adult orang-utan males (flanged and unflanged pooled together) showed higher infestation rates and higher number of parasite types in positive samples than other age-sex classes (Table 1.1). Samples from adolescent orang-utans were the least infested in terms of prevalence and number of parasite types, as already previously shown in wild, free-ranging orang-utans (Mul *et al*., 2007).

Our results also showed that wild orang-utans intensively exposed to research and tourism activities and wild non-habituated orang-utans not exposed to regular human visits had similar infestation rate (65% and 69% respectively of the fecal samples were infested by at least a pathogen), suggesting a rather low occurrence of cross-contamination between people using the forest and orang-utan living in it. Of course, this result is preliminary and warrants more in-depth research to establish differential infestation rate between animals exposed to different types of human pressure.

Table 1.1: Intestinal parasites in different sex-age classes of wild orang-utans living in Kinabatangan.

	Adult males	Adult females	Adolescents
Infestation rate (positive samples)	90.0%	69.0%	56.0%
Average number of types of parasites in positive samples	3.22	2.56	2.29
Infestation by *B.coli*	60.0%	27.8%	29.2%
Infestation by hookworms (eggs)	70.0%	52.8%	12.5 %
Infestation by *E. coli*	50.0%	22.2%	29.2%
Infestation by *Strongyloides* larvae	30.0%	13.9%	20.8%

Rehabilitant orang-utans held in Sepilok are regularly treated with anthelmintic drugs, explaining why the prevalence of hookworms and other metazoan parasites was very low with this group of animals, precluding a direct comparison with untreated wild animals. However, our results showed that captive orang-utans were heavily infested with *B. coli*: 71% of the samples were positive and on average the egg count was higher than in wild animals whereas only 9.5% were positive to *E.coli* (compared to 29.7% with wild individuals).

- **Risks of disease transmission between tourists and habituated orang-utans**

In theory, nature-based tourism has the potential to promote wildlife conservation, to increase local awareness and increase tolerance of wildlife, to address wildlife-human conflicts, and to raise local revenue for protecting great apes (MacFie & Williamson, 2010; Lascurain, 1996; Borrini-Feyerabend *et al*., 2004). But rapid and unmonitored development of ecotourism projects can also have negative impacts on the habitat and on the species we wish to conserve. Human presence can degrade fragile ecosystems and facilitate the introduction of invasive species. It can also disturb the animals and result in behavioral changes and “stress”. Chronic exposure to stressors such as repeated visits by tourists could induce immunodepression, which in turn will increase susceptibility to infectious diseases or decrease reproductive success (Muehlenbein *et al*., 2012). There is accumulating evidence that wildlife populations were negatively affected by tourist visitations (Mullner, 2004; Treves & Brandon, 2005; Ellenberg *et al*., 2007; Martin & Reale, 2008). Regular penetration of the orang-utan habitat by human visitors and repeated close proximity between apes and people could therefore be potentially counterproductive to conservation goals (Chapter 5; MacFie & Williamson, 2010). Recent developments in fecal hormone analysis provide a non-invasive way to assess quantitatively the stress of wild animals in natural and unnatural conditions. Under my supervision, this new technology was successfully applied to better understand how tourism and long-term research could impact the stress level of wild habituated and non-habituated orang-utans in Kinabatangan. The results of this research showed that tourism and long-term research activities can be of little consequence for the stress level of individuals as long as some basic viewing rules are respected (Chapter 5). Being able to quantify the impact of viewing activities on great apes is important since this type of tourism is currently growing in South East Asia and in Africa (MacFie & Williamson, 2010). Once quantified, the impacts can be mitigated through implementing adequate practices (Chapter 5).

To date, all suspected and proven cases of pathogen transmission from human to non-human primates involved local community members, researchers or park personnel but not tourists (Wallis & Lee, 1999). However, despite the absence of an established documentation of disease transmission between tourists and great apes, we should not underestimate this possibility nor forget that tourist sites are regularly patrolled by research assistants, rangers or tour guides who are in frequent contact with the animals (Chapter 5). Indeed, closer proximity between people and orang-utans is likely to increase the risks of cross-species disease transmission (Woolhouse & Gaunt, 2007). There is a need to precisely assess what the real risks of disease transmission between tourists, long-term residents (scientists, rangers, tour guides, local community members, etc.) and visited great apes are in order to design strict guidelines and introduce preventive measures that will minimize sanitary risks for both people who come close to the apes and animals (Wallis & Lee, 1999; Homsy, 1999; Rajaratnam *et al*., 2007; Boesh, 2008; McFie & Williamson, 2010).

To better understand the risks of anthropozoonic infection between tourists and non-human primates, surveys of health and vaccination status were conducted with over 600 tourists visiting the Sepilok Orang-utan Rehabilitation Centre based in Sandakan, Sabah (Muehlenbein *et al*., 2008). The results showed that most tourists were unaware that they could potentially transmit a disease to great apes (Muehlenbein *et al*., 2008). About half of the tourists were not vaccinated against common infectious diseases that are potentially harmful to non-human primates (hepatitis, polio, measles, influenza) and 10.8% self-reported at least one symptom associated with respiratory tract infection (cough, sore throat, congestion) (Muehlenbein *et al*., 2010).

These surveys showed that tourist ignorance over infection risks create an unnecessary risk of disease transmission to non-human primates that are visited at Sepilok and at other tourist destinations (Chapter 5; Muehlenbein, 2013).

7. Structure of the dissertation

The general introduction of this dissertation (Chapter 1) is followed by five successive chapters.

Chapter two: most of the current orang-utan populations in Borneo are found in commercial forest reserves exploited for timber; the future of the species in Borneo will primarily depend on how these non-protected areas are managed in the future. The article "**Recent surveys in the forests of Ulu Segama Malua, Sabah, Malaysia, show that orang-utans (*P. p. morio*) can be maintained in slightly logged forests"** shows that orang-utan abundance in exploited forest depends primarily on extraction intensity and logging practices, as well as on the absence of hunting pressure. Based on the results of intensive surveys that were conducted in several commercial forest reserves, this chapter proposes general guidelines to reconcile timber extraction and orang-utan survival.

Chapter three: A significant part of the orang-utan range in Borneo has been replaced or will be converted to agro-industrial crops. The chapter "**Of pongo, palms, and perceptions – a multidisciplinary assessment of Bornean orang-utans in an oil palm context, Kinabatangan, Sabah, Borneo"** provides new insights on how the orang-utan is able to use oil palm landscapes. The chapter also discusses how this industry could play a bigger (and positive) role for orang-utan conservation and proposes some general guidelines that would make this industry less destructive to the species.

Chapter four: a recent cross-site analysis in Borneo using camera-trap pictures shows that orang-utans are more terrestrial than previously thought, and that all sex-age classes are captured on the ground, irrespective of habitat type and degradation stage. The results of the analysis are presented in "**Coming down from the trees: Is terrestrial activity in Bornean orang-utans natural or disturbance driven?"**. In this chapter we show that the natural life-history of a large, iconic and well-studied species such as the orang-utan can still be a source of surprises. We also raise concerns about what are the sanitary risks of terrestrial behavior in human-transformed landscapes occupied by people.

Chapter five: tourism is often proposed as a venue to promote and to support conservation among local residents. However, the risk of disease transmission between people (local residents, field research assistants and tourists) and orang-utans is a real threat because of their close genetic relatedness. “**Minimizing pathogen transmission at primate ecotourism destinations: the need for input from travel medicine”** highlights the sanitary risks associated with ecotourism activities and the need to develop and to implement proper sanitary guidelines.

Chapter six: Securing viable orang-utan populations in Borneo must incorporate the needs to manage wild populations found outside protected areas. This means moving away from the original vision of protected areas set up in pristine environments, to a system that understands and incorporates the numerous new challenges created by modern development in newly human-transformed landscapes. This paradigm shift requires innovative and alternative conservation strategies involving new partnerships and new thinking. The final discussion explores some opportunities and ways to tackle orang-utan conservation in Borneo.

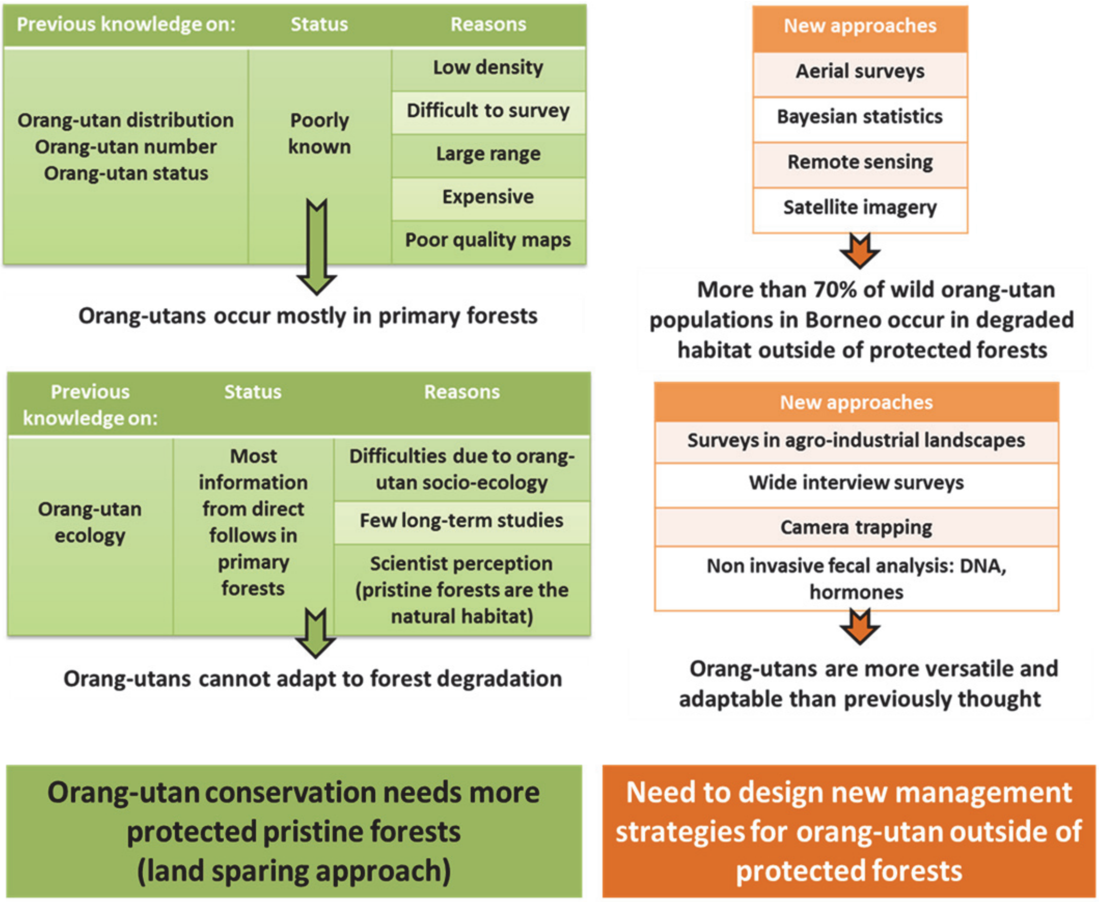


Figure 1.2: Diagram showing the conventional approach for orang-utan research and conservation (green) versus the new “outside-of-the-box thinking” developed in Sabah (Orange).

CHAPTER 2:

Recent surveys in the forests of Ulu Segama Malua, Sabah, Malaysia, show that orang-utans (*P. p. morio*) can be maintained in slightly logged forests.

Ancrenaz, M., Ambu, L., Sunjoto, I., Ahmad, E., Manokaran, K., Meijaard, E., Lackman, I. 2010. *PLoS ONE,* 5(7): e11510. DOI:10.1371/journal.pone.0011510

ABSTRACT

Background: Today the majority of wild great ape populations are found outside of the network of protected areas in both Africa and Asia, therefore determining if these populations are able to survive in forests that are exploited for timber or other extractive uses and how this is managed, is paramount for their conservation.

Methodology/Principal findings: In 2007, the "Kinabatangan Orang-utan Conservation Programme" (KOCP) conducted aerial and ground surveys of orang-utan (*Pongo pygmaeus morio*) nests in the commercial forest reserves of Ulu Segama Malua (USM) in eastern Sabah, Malaysian Borneo. Compared with previous estimates obtained in 2002, our recent data clearly shows that orang-utan populations can be maintained in forests that have been lightly and sustainably logged. However, forests that are heavily logged or subjected to fast, successive coupes that follow conventional extraction methods, exhibit a decline in orang-utan numbers which will eventually result in localized extinction (the rapid extraction of more than 100 m^3 ha^{-1} of timber led to the crash of one of the surveyed sub-populations). Nest distribution in the forests of USM indicates that orang-utans leave areas undergoing active disturbance and take momentarily refuge in surrounding forests that are free of human activity, even if these forests are located above 500 m asl. Displaced individuals will then recolonize the old-logged areas after a period of time, depending on availability of food sources in the regenerating areas.

Conclusion/Significance: These results indicate that diligent planning prior to timber extraction and the implementation of reduced-impact logging practices can potentially be compatible with great ape conservation.

INTRODUCTION

The natural habitat of the orang-utan, the tropical forests of Sumatra and Borneo, are declining at an alarming rate as a result of human activities, such as agriculture and timber extraction. In Borneo, approximately ten percent of the remaining forests are protected for conservation, but it is doubtful that this network of protected areas alone will ensure the long-term survival of the species that leave in these forests (Curran *et al*. 2004; Ancrenaz *et al*., 2007). Early studies have suggested that the orang-utan was dependant on primary forests for survival and that forest exploitation and degradation was resulting in the rapid decline of the species (Rijksen, 1978; Rao & van Schaik, 1997; Rijksen & Meijaard, 1999; Felton *et al*., 2003; Morrogh-Bernard *et al*., 2003; Johnson *et al*., 2005). However, it is increasingly recognized that great apes (including orang-utans) can survive in low-impact and sustainably logged forests (Russon *et al*., 2001; Knop *et al*., 2004; Ancrenaz *et al*., 2005; Meijaard & Sheil, 2007; Husson *et al*., 2009). Considering that more than 75% of the wild orang-utan populations in Borneo are currently found in forests that are exploited for timber (Ancrenaz *et al*., 2005; Wich *et al*., 2008), understanding how orang-utan populations react and adapt to logging is becoming one of the major priorities for conserving the species at the landscape scale. Nevertheless, there is still a general lack of knowledge and information regarding how orang-utans respond to different intensities of timber extraction.

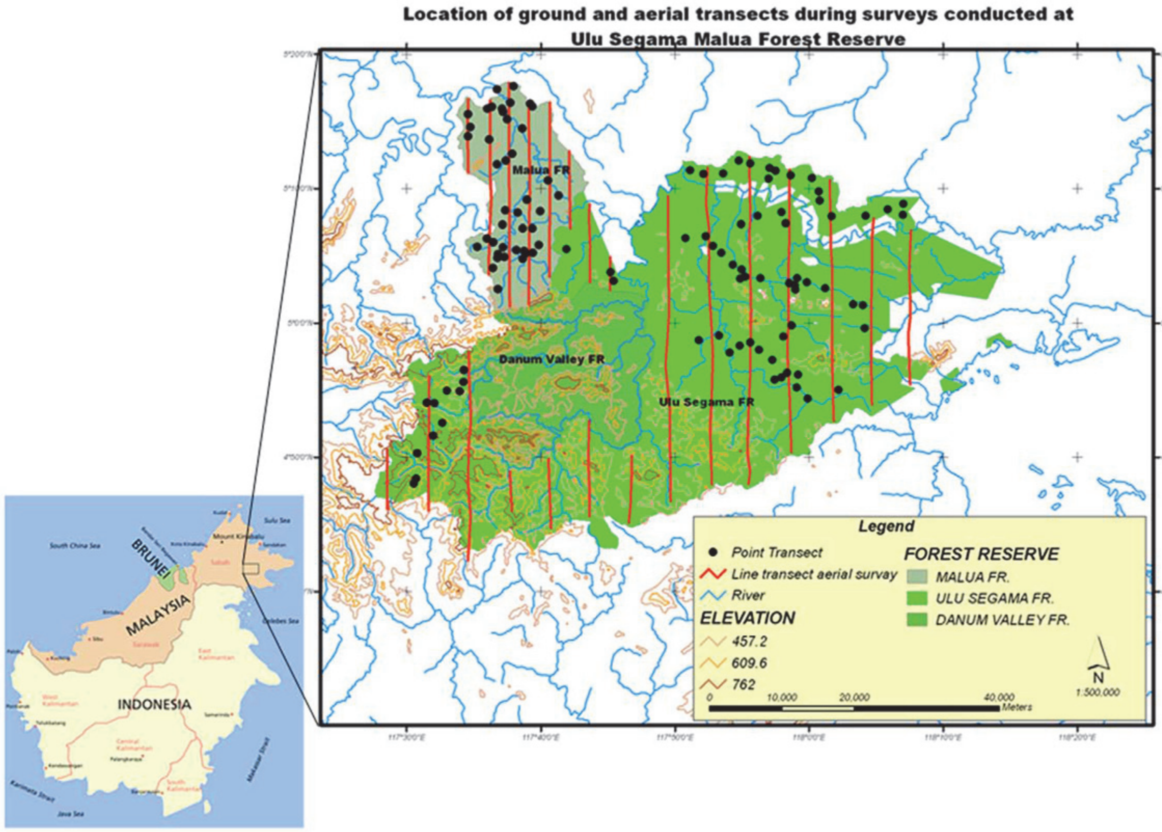
In 2002, our surveys in Sabah established that the commercial forest reserves of the Ulu Segama-Malua-Kuamut-Kalabakan complex were home to approximately 4,500 individuals, making it the largest unfragmented population of wild orang-utans in Malaysia (Ancrenaz *et al*., 2005). These mixed lowland dipterocarp forests are located in the central part of the State and have been exploited for timber since the late 1950s (Sabah Forestry Department, 2008). Acknowledging the importance of the forests of Ulu Segama Malua (USM) for orang-utan conservation, the Sabah State government banned logging for a ten year period at the end of 2007. In 2006-2007, we conducted new aerial and ground surveys in these forests in order to monitor population trends; identify the primary proximate and ultimate factors impacting orang-utan abundance in disturbed forests; document fluctuations of orang-utan abundance in locations exposed to different logging intensities; and to propose that orang-utan conservation should be included in the forest management plan developed for this area.

In this paper we present data on the abundance and distribution of orang-utans in the forest reserves of the Ulu Segama-Malua region that were obtained during our 2006-07 surveys. We seek to determine whether the North Bornean orang-utan subspecies (*Pongo pygmaeus morio*) can maintain viable populations in sustainably and minimally logged forests, at least in the short-term? If so, does a threshold of habitat disruption and degradation exists, where maintaining a viable population becomes impossible?. We discuss some of the possible reasons behind orang-utan resilience and we also provide general recommendations for maintaining populations in forests that are exploited for timber.

RESULTS

Aerial transects

In May 2007, sixteen parallel lines interspaced by about 5 km were flown over Ulu Segama Forest Reserve for a total length of 344.4 km, and eight transects interspaced by approximately 2.5 km were flown over Malua Forest Reserve totaling 140 km (Map 2.1). Therefore, the total survey effort of aerial surveys was roughly 6% of the entire USM area. Land below 450 m asl accounted for 78.7% and land above 600 m asl for 5.8% of our sampling. Fair forest only represented 11.5%, and it was predominantly found on steep and higher ground located in the southern and western side of Ulu Segama, bordering the DVCA, and on the top of steep hills that were not accessible to heavy logging machinery. Highly degraded forests accounted for 52% of our sample and were characterized by the complete disruption of the original canopy structure; an extreme rarity of emergent climax trees; open areas; abundance of old/recent logging roads; and the presence of invading bushes, creepers and pioneer trees belonging to Euphorbiaceae and Rubiaceae families. We applied a correction factor of F_1=0.54 to aerial indexes obtained in this overdegraded habitat to take into account the increased detectability and artificially inflated aerial indexes in overdegraded forests due to canopy openness (Ancrenaz *et al*., 2005). Degraded forests accounted for 11.5%, and areas of active logging for 4.4% (mostly North Ulu Segama and Malua FR). Overall, a total number of 3199 orang-utan nests were recorded. In order to investigate if orang-utan abundance depended on topographical and connectivity features, we pooled the transects in several "Sampling Units": North Ulu Segama (NUS); Segama East; Segama Central; Segama South and West; Malua. Within each sampling unit we then investigated possible fluctuations of density resulting from habitat differences.



Map 2.1: Location of aerial and ground surveys in the forests of Ulu Segama Malua, Sabah, Malaysian Borneo.

<u>*North Ulu Segama (NUS)*</u>*:* the forests of NUS cover roughly 12,000 ha. These forests are surrounded by oil palm plantations in the north and the Segama River in the south. They are highly degraded as a result of over-logging and fires. The last round of timber extraction was taking place in 2007 at the time of our surveys. In most areas the canopy was completely disrupted, few trees were left standing, logging roads and open areas were common, and pioneer trees such as *Macaranga spp*. dominated the landscape. Signs of active or very recent logging activities were widespread and distributed throughout the entire region. Approximately 40% of the aerial transects were flown over lands devoid of trees, considered as unsuitable habitat for orang-utans. Although orang-utan nests were found throughout the entire NUS area, they tended to be concentrated in compartments with the best forest stands or in isolated patches of trees found in the middle of over-degraded and open areas. Nests were slightly more abundant in areas with no active logging (Table 2.I).

<u>*Segama East/Central*</u>: in eastern and central Segama, density increased from the eastern lines (ZYX pooled together: AI = 0.3 nest km^{-1}) to the western lines (WVUT: AI = 2.0 nest km^{-1}): t-test; t = 3.4; df = 5; p = 0.018*. The forests of eastern Segama were highly degraded and harbored

very low nest densities. Nests were more abundant in steeper, higher terrains that had patches of healthier forest and were located further away from active logging activities. In the central parts of Segama, orang-utan distribution was relatively uniform. Their abundance was lower in areas with active, on-going logging activities and maximum in regenerating and healthier forests located upland (>600 m asl), where logging activities occurred over ten years ago. However densities dropped drastically in upland forests that had recently experienced intensive logging (line T: 0.47 ind.km^{-2}). In the past, tall trees were used by orang-utans to cross the Bole and Kawag Rivers, but these water bodies cannot be crossed by the animals following the removal of these trees. By considering the transect lines of the same habitat located on both sides of these rivers, we investigated local differences in nest distribution and abundance. Orang-utans were more abundant on the western rather than on the eastern side of the Bole River (West: L = 22.4 km of line, 139 nests, AI = 3.10 nest km^{-1}, D_{ou} = 1.23 ind. km^{-2}; East: L = 23.2 km, 89 nests, AI = 1.91 nest km^{-1}, D_{ou} = 0.76 ind. km^{-2}), and no difference was found on either side of the Kawag river, but orang-utan density was lower within the Kawag loop, which is more difficult for the animals to access: L = 17.9 km, 62 nests, AI = 1.73 nest km^{-1}, D_{ou} = 0.69 ind.km^{-2}).

Segama South/West: Lines M and S border the south of the protected forests of DVCA in the westmost part of Segama. Part of length O was flown over DVCA and although data is presented in Table I, it has not been included in our final analysis. Fewer orang-utan nests were identified in forests below 450 m asl (AI = 2.95 nest km^{-1}) than above 450 m asl (AI = 5.23 nest km^{-1}), with a difference that is near significance: U Mann and Whitney: z = -1.938: p = 0.053. The lowest nest densities in Segama S/W were recorded in lowland areas that have been highly disturbed by active and recent logging operations, and in areas highly invaded by *Macaranga sp*. Primary and old regenerating forests found in the highlands were the least disturbed habitat due to the steep slopes that are characteristic of this habitat, which limit and prevent conventional logging practices. These forests were home to the highest orang-utan densities recorded in Segama FR with about 2.1 ind. km^{-2}.

Malua FR: Heavy logging occurred in Malua until the end of 2007, and most forests appeared degraded (43.4% of the total aerial length) or overdegraded (56.6%). Orang-utan abundance was higher in degraded (D_{ou} = 1.76 ind. km^{-2}) rather than in overdegraded forests (D_{ou} = 1.00 ind. km^{-2}). The highest density with about 2.4 ind. km^{-2}was recorded in the forests of the “Bornean Biodiversity Conservation Plot” that appeared to be in very good condition. These forests are mature secondary forests and show a relatively diverse tree composition and structure. Orang-utan nests were more abundant on the western side of the Malua River (lines ABCD, 33.8 km, AI = 5.65 nests km^{-1}, D_{ou} = 2.21 ind. km^{-2} *versus* lines CDEF, 57.9 km, AI = 3.97 nest/km, D_{ou} = 1.57 ind. km^{-2}) and in the northern region (D_{ou} = 2.02 ind. km^{-2}), than in the southern area (D_{ou} = 1.20 ind. km^{-2}) or in the overdegraded forests of the “Wildlife Corridor” that is located in the south-eastern part of Malua (D_{ou} = 1.00 ind. km^{-2}).

Table 2.1: General results of aerial surveys in the five sampling units distinguished in the Ulu Segama Malua Forest Reserves.

Area	Transect	Length	Aerial Index	Habitat Type	Length (km)	Aerial Index	OU density (ind./km^2)
North Ulu Segama	**(UVWXY) north**	**20.5**	**4.169**				**1.52 (0.5-4.1)**
				Overdegraded	11.4	4.77	1.90
				Active logging	10.3	3.54	1.40
Segama East	**XYZ**	**70.0**	**0.302**				**0.13 (0.04-0.39)**
	X	24.7	0.445	Overdegraded	42.5	0.294	0.12
	Y	23.8	0.252	Degraded	15.5	0.452	0.19
	Z	21.5	0.209	Active logging	2.5	0.258	0.11
				Below 450 m asl	55.2	0.302	0.12
				450-600 m asl	7.8	0.446	0.18
Segama Central	**TUVW**	**147.6**	**1.98**				**0.79 (0.29-2.16)**
	W	35.7	1.110	Overdegraded	49.5	2.14	0.85
	V	40.9	1.501	Degraded	47.1	2.44	0.97
	U	41.0	2.739	Active logging	16.1	1.05	0.43
	T	30.0	2.652	Macaranga	18.7	1.41	0.57
				Fair forest	16.2	1.76	0.71
				Below 450 m asl	124.0	1.87	0.75
				450-600 m asl	23.6	1.16	0.47
				Above 600 m asl	12.3	2.72	1.09
Segama South West	**MNOPQRS**	**92.7**	**4.47**				**1.76 (0.64-4.80)**
	S	8.3	2.590	Overdegraded	14.9	3.425	1.35
	R	12.9	2.054	Degraded	7.0	6.143	2.40
	Q	9.3	7.150	Macaranga	6.45	1.938	0.78
	P	6.4	5.469	Active logging	3.3	2.424	0.97

	O	29.0	3.931	Fair forest	25.5	5.686	2.23
	N	18.1	6.022	DVCA	14.3	4.410	1.73
	M	8.7	4.770	Below 450 m asl	35.55	2.951	1.17
				450-600 m asl	40.5	5.290	2.07
				>600 m asl	15.8	4.652	1.83
Malua	**ABCDEFGH**	**140.0**	**4.169**				**1.64 (0.58-4.52)**
	H	4.0	3.24	Overdegraded	14.2	2.510	1.00
	G	10.2	2.223	Degraded	122.5	4.488	1.76
	F	10.0	2.268	Fair forest	3.5	6.156	2.41
	E	23.7	4.641	Below 450 m asl	136.0	4.276	1.68
	D	27.8	7.262	>450 m asl	4.0	1.720	0.69
	C	30.6	5.224				
	B	24.0	3.353				
	A	9.7	7.509				

Ground transects and nesting sites

Line transects were conducted for ground truthing of the aerial data and for investigating local variations of orang-utan abundance. We performed a total of 106 ground line transects (total length of 79.4 km; average length: 742 m; range: 170-1710 m) over nine expeditions throughout USM between August 2006 and June 2007 (survey effort of 0.06%): Table 2.2. During this time we recorded a total of 1111 orang-utan nests built in a minimum of 35 families and 65 taxa of trees (18.0% of nesting trees were not identified, adding an unknown number of families and taxa as possible nesting site): Table 2.3. Four tree families and 4 genera represented 62.2% and 55.2% of all nesting sites respectively. When we considered the eight families most often used for nesting, we found no significant difference between choice of tree species for nesting and family abundance in the forest (values of Wilcoxon tests are given in Table III). However, in highly disturbed forests, orang-utans preferentially used pioneer trees like *Neolamarckia cadamba* (40.1% in Malua and 19.4% in NUS) or *Pterospermum sp.* (4.0% and 38.4%). In the contrary *Shorea sp.* (18.2%) and mature *Macaranga sp.* (13.7%) were preferentially used as nesting sites in the less degraded habitats or in the old-logged forests of Segama. For each survey site, we classified the forest into two major classes of habitat disturbance: degraded and overdegraded. Compared to degraded forests, overdegraded forests were characterized by: more logging roads (5.5 vs 3.4 roads/km of transect, although the difference was not significant: t-test value = 1.19; df = 8; p = 0.26); a significant lower basal area (8.0 vs 16.3 m^2/ha: t-test = -5.51; df = 80; $p < 0.0001$*); and a significant lower tree density (142.7 vs 214.6 trees dbh>10 cm/ha: t-test = -3.85; df = 80; p = 0.0002*). Variations of orang-utan density between overdegraded and degraded habitat were tested for in each expedition where the two types of habitat were present (n=5). Densities were significantly higher in degraded (general average of 2.23 ind. km^{-2}), versus overdegraded forests (1.36 ind. km^{-2}): paired-sample t-test, df = 3, t = 6.79, p = 0.007*. Ground truthing of aerial data was achieved by (1) pooling together all ground transects from different expeditions that were run in the same area, in similar habitat type where no significant difference in encounter rates were detected; and (2) comparing these with aerial orang-utan densities obtained over corresponding areas (n=6 sites). Results given in Table 2.4 show a very strong correlation (r = 0.975) and no significant difference between the two data sets (paired-sample t-test: n = 6; t = 1.929; df = 5; p = 0.11).

The total orang-utan population size living in USM was obtained by combining the knowledge gained from aerial and ground transects and by following the stratification pre-established from our aerial lines: Table 2.5, Map 2.2. Our final estimate is that there are 2,580 orang-utans (968-7275) in the forests of Ulu Segama Malua.

Table 2.2: Location, main characteristics, orang-utan densities (with associated Coefficient of Variation) of all ground surveys conducted in the USM forests (Legend: Deg.: degraded; Overdeg: over-degraded; asl: above sea level; n/a: not available; Nb plots: number of botanical plots; CV: coefficient of variation obtained by Distance).

XPDC	Location	Type	LTs	Length (km)	Altitude asl	Road Index	Basal Area (Nb plots)	Tree Density per ha	Orang-utan density (CV)
1	Malua South	Deg.	5	4.515	250-450	n/a	n/a	n/a	1.36 (34.6)
		Overdeg.	7	4.294	250-450	n/a	n/a	n/a	0.69 (33.3)
2	Malua NW	Deg.	2	2.100	200-450	6.2	4.8 (2)	90	3.18 (10.7)
		Overdeg.	2	1.000	200-450	3.3	2.5 (2)	105	1.89 (69)
	Malua NE	Deg.	7	4.647	200-450	1.1	17.4 (9)	232	1.40 (29.1)
3	Segama SE	Deg.	5	4.509	300-450	7.1	15.4 (4)	172.5	1.23 (26.4)
4-5	Segama NE	Deg.	8	6.847	300-450	2.2	21.2 (7)	294	1.8 (23.3)
		Overdeg.	19	8.878	300-450	4.5	10.2 (12)	153	0.4 (34.5)
6	Segama SW	Deg.	8	9.617	350-650	3.1	11.2 (8)	161	2.1 (22)
		Overdeg.	7	6.813	350-650	9.4	9.8 (6)	107	0.7 (25)
7	Malua NW	Overdeg.	9	6.316	200-450	3.5	9.9 (8)	151	1.61 (14.5)
8	Malua NE	Overdeg.	14	11.510	200-450	8.2	8.2 (13)	163.5	2.22 (23)
9	NUS	Overdeg.	13	8.311	200-450	2.1	4.7 (11)	110	2.72 (14.7)

Table 2.3: Percentage of utilization of the eight most common tree families and taxa used for nesting and percentage of tree abundance recorded in 69 botanical plots in three different areas: Malua, Segama and North Ulu Segama.

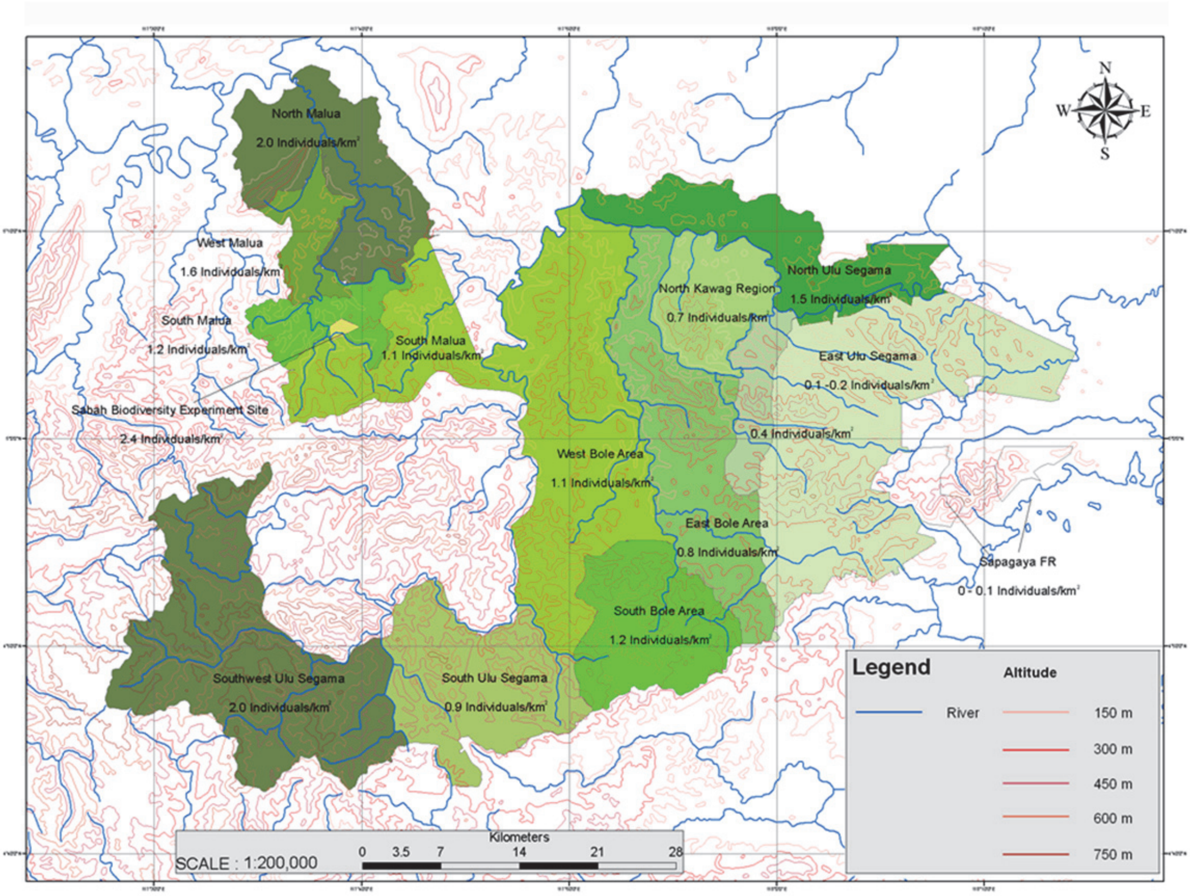
	Total		**Malua**		**Segama**		**NUS**	
Number	*Nests*	*Trees*	*Nests*	*Trees*	*Nests*	*Trees*	*Nests*	*Trees*
	1111	*1056*	*513*	*477*	*392*	*436*	*206*	*143*
Dipterocarpaceae	**15.1**	**27.0**	**12.4**	**29.2**	**22.4**	**29.9**	**8.1**	**11.2**
Shorea sp.	*11.5*	*19.6*	*8.6*	*18.5*	*18.2*	*24.8*	*6.2*	*7.7*
Other taxa	*3.6*	*7.4*	*3.8*	*10.7*	*4.2*	*5.1*	*1.9*	*3.5*
Ebenaceae (*Diospyros sp.*)	**1.3**	**2.3**	**1.3**	**2.1**	**2.0**	**2.1**	**0.0**	**3.5**
Euphorbiaceae	**10.0**	**10.4**	**6.7**	**10.1**	**15.2**	**9.0**	**8.6**	**16.1**
Macaranga sp.	*8.2*	*8.2*	*4.2*	*6.5*	*13.7*	*8.3*	*8.1*	*14.0*
Other taxa	*1.8*	*2.2*	*2.5*	*3.6*	*1.5*	*0.7*	*0.5*	*2.1*
Fagaceae (*Lithocarpus sp.*)	**4.4**	**1.9**	**1.5**	**1.7**	**10.0**	**2.8**	**1.0**	**0**
Moraceae (*Ficus sp.*)	**1.1**	**0.8**	**1.0**	**0.6**	**1.2**	**0.9**	**1.4**	**0.7**
Myrtaceae (*Eugenia sp.*)	**2.9**	**3.0**	**1.7**	**3.1**	**4.5**	**3.4**	**2.8**	**1.4**
Rubiaceae	**24.5**	**6.8**	**42**	**10.1**	**3.2**	**0.8**	**21.3**	**13.3**
Neolamarckia cadamba	*22.9*	*4.9*	*40.1*	*8.0*	*2.2*	*0.5*	*19.4*	*8.4*
Other taxa	*1.6*	*1.7*	*1.9*	*2.1*	*1.0*	*0.3*	*1.9*	*4.9*
Sterculiaceae (*Pterospermum sp.*)	**12.6**	**7.1**	**8.7**	**3.6**	**4.0**	**3.7**	**38.4**	**29.4**
Other tree families	**28.1**	**40.9**	**24.7**	**39.6**	**37.5**	**47.7**	**18.4**	**24.5**
Wilcoxon test values	z=-0.059; p=0.953		Z=-0.652; p=0.515		Z=-1.601; p=0.109		Z=-0.059; p=0.953	

Table 2.4: Orang-utan density estimates achieved during ground and aerial surveys over corresponding areas.

Areas	Estimated ground density	Estimated aerial density
Kawag (4-5th XPDC)	1.1	0.8
Silviculture area (3rd XPDC)	1.2	0.8
West Segama (6th XPDC)	2.7	2.4
South Malua (1st ; 7th XPDC	1.1	1.2
North Malua (2nd; 6th SPDC)	2.05	2.0
Sebagaya (4th XPDC)	0.1	0.1

Table 2.5: Number of orang-utans living in the USM forests estimated from the combination of ground and aerial surveys.

Area Code	Size (km^2)	Location	Density	95% CI	Orang-utan Number	95% CI
1	16.24	Sepagaya	0.05	0.0-0.15	1	0-2
2	33.84	WCA	0.05	0.0-0.15	2	0-5
3	381.76	BW 7/03 – Taliwas – west BW 7/02 – west BW 7/01	0.15	0.05-0.4	57	19-173
4	51.84	Central BW 7/02	0.4	0.14-1.12	21	7-58
5	98.08	Kawag loop – BW 7/03 and BW 7/04	0.7	0.25-1.92	69	25-289
6	216.16	East Bole River	0.8	0.29-2.19	173	63-474
7	462.88	West Bole River – Wildlife Corridor – South Malua	1.1	0.40-3.0	509	187-1387
8	150.72	West BW 7/01 – East BW 7/00	1.2	0.44-3.27	181	66-493
9	187.28	BW 7/00 – DCVA buffer	0.9	0.33-2.46	169	62-460
10	115.1	North BW 7/04 (NUS)	1.5	0.55-4.02	172	84-622
11	340	BW 7/99 – DCVA buffer	2	0.73-5.47	680	248-1861
12	173.2	North Malua	2	0.73-5.47	346	127-948
13	50.48	YS 3/03	1.6	0.58-4.36	81	30-220
14	56.08	South-west Malua	2	0.73-5.45	112	41-306
15	2.72	Borneo Biodiversity Plot	2.4	0.87-6.59	7	2-18
TOTAL					**2580**	**1295-5866**



Map 2.2: Orang-utan densities in the different areas of Ulu Segama Malua forests identified during the 2007 survey.

DISCUSSION

It is now well established that estimating great ape abundance from nest densities can yield highly imprecise results due to the fluctuation in the nest decay rate values, amongst other factors (Mathewson *et al.*, 2008). Repeated nest counts are one way to reduce imprecision but the time required in these exercises further reduce the areas being investigated by surveyor teams (Kuehl *et al.*, 2008). In addition, monitoring the large areas that are typically occupied by great ape populations require major efforts that are difficult to match in the field due to financial, human and time constraints. Aerial surveys offer an interesting and cost-effective alternative to monitor orang-utan populations at the landscape level (Ancrenaz *et al.*, 2005).

Combining ground and aerial surveys achieved a precise knowledge about the distribution, abundance and some of the factors influencing the orang-utan population living in the degraded forests of Ulu Segama Malua. Aerial surveys increased the general survey effort to 5.8% of the entire survey area, which is one of the highest scores documented for great apes (Ancrenaz *et al.*, 2004b) and is above the limit of 0.26%, recently proposed to achieve reliable nest abundance estimates (Boyko and Marshall, 2010). A strong correlation was obtained between aerial and ground results, further validating the model recently developed in Sabah (Ancrenaz *et al.*, 2005). The discrepancy between aerial and ground indices identified in the forests of North Ulu Segama (NUS) was explained by the extreme degradation of this habitat. Because this area is a mosaic of trees left standing in bare land, ground line transects were predominately located in forested areas, while bare landscapes were typically avoided, in order to optimize time spent in the field. Therefore, orang-utan estimates were only available for forested areas and achieved a high score of 2.72 ind. km^{-2}, without considering unsuitable habitat. On the contrary, aerial surveys covered all habitat types, forested or not, which resulted in an overall lower density (1.52 ind. km^{-2}) compared to the ground data. Since our flights indicated that only 60% of the habitat was suitable for orang-utans, we used this stratification factor and ended up with similar population size estimates for NUS for ground ($2.72 \times 0.6 \times 120\ km^2 = 194$ orang-utans) and aerial data ($1.52 \times 120 = 182$ orang-utans).

Our surveys in 2007 in the forests of USM yielded similar population estimates (2,600 individuals) to our 2002 surveys (2,300 individuals; 95% confidence intervals between 1,744 and 3,657), indicating that this population has been relatively stable over this five-year period. However, this general picture hides fluctuations that are occurring at geographical and local scales throughout the entire landscape. The uneven orang-utan abundance in USM results from the interaction of historical, man-made and natural features.

Orang-utan abundance and human history

The scarcity of orang-utan nests identified in the eastern forests of USM (densities comprised between 0 and 0.2 ind. km^{-2}) can be related to the regional human history. Eastern Sabah has been inhabited for approximately 30,000 years, based on the earliest signs of human occupation in the State (Marsh, 1995), and small human communities have been permanently established along the lower part of Segama River for centuries (Harrisson & Harrisson, 1971). During this time, people were venturing into the upper parts of Segama for hunting expeditions and to take refuge in times of trouble and epidemics (Pryer, 1883). Trading with China and other nations blossomed in the 15th century, targeting forest products and animal parts (rhinoceros horns, nests of swiflets, hornbill skulls etc.). Hunting orang-utans for meat, traditional medicine and for skulls (after the ban of human head-hunting), might have taken its toll on the original population in this area, and possibly led to local extinction. Currently, orang-utan densities in lower Segama are at their lowest close to well-established villages (SFD, 2008), as has been shown for other orang-utan populations that are subjected to hunting pressure (Marshall *et al*., 2006). Orang-utans are slow breeders and any given population will go extinct if the yearly hunting level exceeds 1% of a particular population (Marshall *et al*., 2009). In addition to the probable impact of past hunting pressure, our botanical plots revealed that the eastern forests of USM were heavily disturbed, which was identified by the lack of medium and large sized trees, a low basal area, the over-abundance of pioneer tree species and the extreme rarity of sizeable dipterocarp trees and other mother trees. These findings indicate that past fires or clear-cutting during previous logging cycles have ravaged these forests and may have wiped out local orang-utan sub-populations.

Orang-utan abundance and natural features

Orang-utan densities were higher in the west than in the east, and reached 2.0 to 2.5 ind. km^{-2} in some parts of Malua and southwest Segama. However, very few nests were recorded in limestone habitats and in forests growing on ultra basic soils originating from Bidu Bidu and similar associations. The lack of sodium and the relative abundance of nickel, chromium and cobalt characteristic of these soils limits the growth of many plant species, resulting in a less diverse tree community with fewer food resources than other forest types, which accounts for the lower nest abundance in these suboptimal orang-utan habitats (Marshall *et al*., 2007). Large bodies of water, such as the Segama River, represent a barrier to orang-utans dispersal (Goossens *et al*., 2005; Goossens *et al*., 2006a). Orang-utan abundance showed differences on both sides of the Malua, Bole and Kawag Rivers, indicating that these bodies of water may act as potential barriers for dispersal following felling of large trees that originally acted as natural bridges (Figure 2.2; Table 2.5). In Borneo, orang-utan densities usually decrease with altitude and drop sharply above 500 m asl (Mac Kinnon, 1974; Payne, 1988; Rijksen & Meijaard, 1999; Djojosudharmo & van Schaik, 1992). However in USM, high concentrations were locally recorded above this threshold in several areas (2.7 ind./km^2 in Segama Central; 1.8 ind./km^2 in Segama SW), while densities were significantly lower in surrounding lowland forests (Table 2.1). In most cases, logging activities had recently occurred or were taking place concurrently to our surveys in the surrounding lowland forests. We can therefore hypothesize that logging resulted in the forced migration into the less preferred highland forests, where orang-utan populations sought "refuge" by leaving disturbed areas (Mac Kinnon, 1974; Ancrenaz *et al*., 2005). In large parts of southwest USM with no signs of recent logging in surrounding lowlands, valleys and ridges located above 450 m asl harbored about 2 individual km^{-2}. These highland forests were lightly logged 15 years ago, but their tree diversity, size, height and canopy cover achieved the best scores among all of the survey sites, indicating that these are mature habitats or forests in a healthy regeneration stage. Oak trees belonging to the Fagaceae family (*Lithocarpus spp*.) were particularly common and were fruiting shortly before and during surveys. Acorns are one of the favored orang-utan foods (Russon *et al*., 2009), and their abundant production could have attracted animals from lower lands, possibly explaining the seasonally inflated orang-utan abundance in these hills (Singleton, 2000).

Orang-utan abundance and logging

Overall, the habitat found in USM is very heterogeneous. This is a result of conventional logging practices and heavy extraction rates, coupled with high road densities and indiscriminate felling, that has led to a mosaic of highly degraded forests bordering hilltops and isolated patches of moderate habitat in a chaotic pattern. This condition results in extremely patchy and uneven nest distribution resulting in the large variation in nest encounter rates between ground transects located in the same survey areas, or in aerial scores fluctuating by more than 30 nests between two successive observation periods of 30 seconds (representing a distance of about 500 m). Orang-utans feed on a wide range of plants (Marshall *et al*., 2009b), but their density is limited by the frequency and duration of periods of food shortage and is correlated with fruit abundance during periods of low fruit availability (Marshall *et al*., 2009b). Therefore, sites experiencing extreme periods of food shortages support lower population densities. In response to fruit shortages orang-utan's shift their diet to non-fruit sources and more fibrous vegetation like leaves and barks (Rijksen & Meijaard, 1999), and alter their range patterns in order to exploit alternative food resources (Singleton & van Schaick, 2001). In Borneo, forests dominated with dipterocarps experience extreme temporal fluctuations in fruit availability; dipterocarp abundance is negatively correlated with orang-utan abundance at many sites (Husson *et al*., 2009). Sustainable and selective logging typically targets a small number of trees that are primarily Dipterocarps. After felling, timber species are replaced by pioneer and asynchronous trees (such as *Dracontomelon sp., Ficus sp., Neolamarckia cadamba*, etc) and light-demanding woody climbers (*Spatholobus sp., Uncaria sp*., etc). By fruiting more frequently than climax tree species and by providing young leaves and bark, these pioneer plants are supplying new and alternative food sources that buffer periods of food scarcity. In addition, exploited habitats experience changes in fruiting event patterns and species such as *Garcinia sp*. and *Litsea sp*., which are part of the orang-utan diet, will bear more fruit during this time, providing additional resources to the animals (Marshall *et al*., 2009b).

Our results show that in USM, lightly logged forests supported relatively high orang-utan densities that were occasionally higher than those encountered in some primary lowland mature forests (see Table 2.1). Forests that were only logged once, over15 years ago, supported the highest orang-utan densities during our surveys, showing that orang-utans recolonize old regenerating forests and can re-establish densities similar to or even exceeding pre-logging conditions (Russon *et al*., 2001; Husson *et al*., 2009). Densities documented close to the Bole River during our surveys (around 2 ind./km^2) are comparable with orang-utan abundance documented when these forests were still pristine (Mac Kinnon, 1974), indicating that orang-utans have maintained their numbers in this area even though it has been subjected to 40 years of logging activities. However, forest patches with active disturbance systematically yielded lower orang-utan densities than surrounding forest that were not exploited at the time of our surveys, suggesting that the animals take refuge in less disturbed areas as suggested by Mac Kinnon (1974). Recolonization of previously logged areas will depend on the intensity of logging activities and the regeneration dynamic of the forest. The two most abundant pioneer trees identified during our surveys were *Macaranga sp.* (Euphorbiaceae) in Segama and *Neolamarckia cadamba* (Rubiaceae) in Malua. *Macaranga* colonizes quickly in clear-cut areas and old logging roads and has the ability to outgrow other tree species, resulting in sizeable pure stands in the most degraded areas. These trees produce wind-dispersed seeds and offer very little food resources to the fruit eating community. *N. cadamba* on the contrary, produces both fruit and bark that are edible and consumed by orang-utans. In Malua, we recorded numerous signs of bark consumption and a huge proportion of nests built in these trees (Table 2.3). *N. cadamba* with its spaced crown also does not restrain other trees from colonizing the areas, which helps to maintain a more bio-diverse forest within a localized area. Orang-utan density was significantly higher in areas of *N. cadamba* growth than in *Macaranga* dominated areas (1-2 individuals km^{-2} versus 0.1-0.4 ind km^{-2}). Because of lower food availability in *Macaranga* dominated regions, orang-utans have to forage over a much larger area, which results in lower densities in these forests.

At all survey sites, extremely damaged habitats yielded fewer nests than lightly logged forests (Table 2.1). Mechanical logging inflicts structural and incidental damages to all tree size-classes (Johns, 1988) and heavy logging results in impoverished forest composition (fewer tree diversity, fewer food sources) and structure (lower tree density, basal area and canopy height, absence of tall trees and contiguous canopy). The destruction of fallback food sources such as *Ficus sp*. and other key plant species in overlogged areas further impoverishes the habitat and induces significant orang-utan population decline. Simplification of the forest and destruction of the original forest mosaic, force orang-utans to either use a larger range or to adopt a “sit and wait” strategy to save energy and to digest more fibrous food (Morrogh-Bernard *et al*., 2009). When food resources are destroyed over large areas, this leads to a drastic decline, as documented for the orang-utan sub-population found in the NUS area. This sub-population is completely isolated from the main population by large oil palm plantations and by the Segama River. In 2002 before the latest logging cycle, the NUS forests were already highly degraded as a result of past fires and logging activities but they were still home to approximately 400 individuals (Ancrenaz *et al*., 2005). Whereas in 2007, our estimates found that there were less than 200 animals in these same forests. This decline was due to the most recent logging cycle, which left an extremely degraded habitat with acutely low tree densities and basal areas, extensive openings in the canopy and very few food resources besides the leaves and bark of pioneer plants.

Eastern Borneo suffers the most from the El Nino Southern Oscillation events and from the resulting droughts, fires and periods of food scarcity (Mac Kinnon *et al*., 1996; Siegert *et al*., 2001). As a result, orang-utans have to survive on alternative food sources such as barks and leaves for extensive periods of time. Some anatomical features of the North eastern Bornean subspecies *P.p.morio* (more robust jaw bones, thicker teeth enamel, smaller skull size) could possibly be related to the specific ecological traits of the region (Taylor, 2009). It has been hypothesized that these anatomical features may predispose this subspecies to cope better with habitats with fewer fruit sources that have abundant fibrous fallback foods that are typical of lightly exploited forests (Husson *et al*., 2009; van Schaick *et al*., 2009).

However, the wide dietary flexibility of the species as shown by the number of plants included in their diet (Russon *et al*., 2009), their intimate knowledge of the forest and their faculty of storing fat when food is abundant in the forest (Knot, 1998) are major factors accounting for the possible adaptation of the species to some level of habitat disturbance.

CONCLUSION

Our surveys in USM show that orang-utan populations can be maintained in lightly and sustainably logged forests but decline and are eventually driven to localized extinction in forests that are heavily logged or subjected to fast, successive coupes following conventional extraction methods. For example, the rapid extraction of more than 100 m^3 ha^{-1} of timber, led to the crash of the sub-population found in the NUS forests.

Considering that the majority of great apes are currently found outside of protected areas in Africa and in Asia, it is clear that conserving these iconic species requires the establishment of a viable network of protected forests among a mosaic of certified logging concessions and other suitable habitats (van Kreveld & Roerthorst, 2009; Meijaard *et al*., 2005). However the orang-utan conservation community is not necessarily ready to seriously support the idea of conserving orang-utans in working timber concessions. This is partly due to the strong belief, to some extent based on empirical evidence, that all logging harms orang-utans (Rao & van Schaik, 1997; Husson *et al*., 2009), and that therefore conservation of the species in timber concessions was not an option. Another factor may be that many conservationists find it difficult to entertain the notion of protecting a species in a forest that is not managed primarily for conservation purposes (Sheil & Meijaard, 2010), even if orang-utans can survive in such habitats. We emphasize that with the majority of orang-utans occurring outside protected areas, and often in timber concessions, long-term protection of the species will require working closely with the timber industry and with concession managers. Not only are such programs more cost-effective than establishing new protected forests, they are also more likely to get support from government and other stakeholders (Wilson *et al*., 2010).

To make orang-utan conservation in timber concession work, several crucial steps are required. The key recommendations for reconciling logging practices and orang-utan conservation, is the creation, preparation and implementation of a precise, pre-harvesting conservation management plan, in order to reduce incidental damages during felling and the adoption of reduced-impact logging practices (following the “Forest Stewardship Council” or another internationally recognized body) that will be followed during all exploitation phases. Priority will be placed on a strictly enforced, zero-hunting policy, as it has been shown that the poaching of orang-utans (or other great apes) will inevitably lead to population extinction. Crucial ecological resources (like riparian forests or patches of rich lowland forest) need to be identified and set aside from exploitation compartments, and major food resources (like large fruit tree and key staple food plants like *Ficus sp*. and large climbers) must be protected from possible damages. Compartments to be exploited should follow a rotation system that allows for the creation of “refuge areas” that can be used by animals when they leave the vicinity experiencing active disturbance. Areas badly impacted by extraction activities (like stumping grounds or major logging roads) need to be rehabilitated and replanted with a mixed array of fast-growing fruit and timber trees, in order to enhance food resources in the forest. In silviculture treatment areas, large woody climbers that produce leaves and bark that are consumed by orang-utans and enable them to move throughout the forest, should not be cut. Finally, a thorough orang-utan bio-monitoring program must be developed and implemented to document population trends and their fluctuations in response to different logging regimes. If such management practices become standard practice in all remaining unprotected orang-utan habitats, chances of long-term survival of orang-utans in the wild would significantly increase.

MATERIALS AND METHODS

Physical features of Ulu Segama Malua

The block of Ulu Segama/Malua (USM) is located in south central Sabah between 116°28' E and 4°14'N: it comprises the commercial forest reserves of Ulu Segama (202,856 ha) and Malua (33,969 ha), as well as four protected virgin jungle forests totaling 4,273 ha (Map 2.1). The USM landscape is primarily below 600m asl and consists of a variably steep terrain, with many hills and ridges that reside over the plains which are typically located close to the large rivers (Segama, Bole, Kawag). Slopes above 25% cover 10% of the entire USM system and steep hills reaching 1250 m asl are concentrated in the areas surrounding "Danum Valley Conservation Area" (DVCA). Malua's topography is predominately flat and low except for a lone hill reaching roughly 700 m asl on its western flank and the higher land located close to DVCA. Geologic formations in USM include: crystalline basement originating from metamorphic and igneous rocks of the lower Triassic which are predominantely located along rivers; Chert-Spilite sandstone from the late Cretaceous; and younger sedimentary and volcanic rocks from the formation of the Kuamut area. Most of the soils are acidic, with a pH ranging from 3.6 to 5.4, are easily eroded and lose nutrients rapidly when they are disturbed. The wet tropical climate is created by the Indo-Australian monsoon system, the average annual temperature is 27°C (with an average maximum and minimum temperature of 31°C and 23°C respectively), and rain is brought in by the northerly winds from December to March. From 1976 to 1996, annual rainfall varied between 1775 mm to 3708 mm, with regular deficits every few years (El Nino). These droughts can be severe and result in intense tree mortality and fires (Walsh, 1996).

Forest exploitation and forest types

Three major forest types occur naturally in USM and all are dominated by dipterocarp trees. The Lowland Mixed Dipterocarp Forest (LMDF) is typically found below 500 m asl. Common families include Dipterocarps (representing at least 60% of the basal area and 30% of the total tree density), Tiliaceae and Sapotaceae. Upland Mixed Dipterocarp Forests (above 500 m) are characterized by the abundance of Fagaceae (oak trees). Ultramafic Forests are found on the ultra-basic soils of the Bidu-Bidu formation that are deficient in phosphorus, potassium and calcium, are floristically less diverse and are of lower stature than other forest types. Throughout the entire landscape, the original forest structure and integrity has been altered drastically following multiple logging cycles that began in 1957 and finished at the end of 2007. The first round of logging (1957-1999), produced roughly 22 million m^3 logs from Ulu Segama (estimated production of 87.5 m^3/ha) and 2.5 million m^3 logs from Malua (65.5m^3/ha). The second round of logging, which was initiated in 1999 and completed in 2007, concentrated on approximately 105,000 ha in Ulu Segama and 20,000 ha in Malua and produced a significantly lower yield of 46.5 m^3/ha in Ulu Segama and 33m^3/ha in Malua (SFD, 2008). Only a few protected areas escaped logging activities, namely DVCA and parts of Kawag Gibong and Sepagaya Virgin Jungle Forest Reserves. In addition, some of the logged forests were damaged by fires during major droughts induced by El Nino events. More than 5,000 ha were burned in Northern Ulu Segama (NUS) in 1983. In general, burnt areas become open land that are devoid of trees and are dominated by herbs and shrubs, with few or no signs of natural forest regeneration. However, patches of isolated, fire resistant, and regenerating pioneer species and trees from the old forest can be interspaced in this landscape (Marsh, 1995).

The USM forests are currently classified into five different classes based on the density of trees> 40 cm dbh (diameter at breast height), estimated from their crown size and visual interpretation of color aerial photographs. This approach provides a quick assessment of the potential commercial timber value of a forest (SFD, 2008). The central part of USM forests (198,000 ha or 82%) are classified as very poor (i.e. less than 10 trees>40 cm dbh/ha, yielding less than 20 m^3timber/ha), while about 23,000 (12%) ha are considered moderate to poor strata (between 10 and 30 trees 40 cm dbh/ha) and only 5% (or 13,000 ha) are considered good forest. Overall, more than 3% of USM is completely open and devoid of trees, and canopy cover is less than 30% in over 70% of USM. Low-lying and easily accessible areas have been particularly damaged by extensive and repeated coupes. These areas are characterized by: prolific signs of past human exploitation (tractor roads, stumping grounds, erosion, etc); an extremely low basal area and low tree density; a highly disrupted canopy with large forest gaps; and an abundance of invasive and pioneer plant species.

Survey methodology

The USM surveys combined ground and aerial data collection. Ground transects were randomly located on topographical maps (1:50 000) then ran on the ground. When possible, their direction was roughly perpendicular to large rivers, hills and major roads, in order to reduce between-transect variations and to achieve more reliable density estimates (van Schaik *et al*., 1995; Cassey and McArdle, 1999). Transect length was directly determined using a walking-distance measuring device: along each transect a team of two cleared a straight line-path and confirmed the bearings with a compass, while a second team of three recorded information on forest type, general level of habitat degradation and nest presence. For each nest observed, we measured the perpendicular distance from the transect and recorded size, dbh, species of the nesting tree, as well as its approximate age (Ancrenaz *et al*., 2004a). Botanical plots (10 x 50 m) were randomly selected along the transects in order to characterize forest structure and composition. In all of the plots we identified the family or taxa levels of the trees with a dbh>10cm, recorded canopy height, climbers abundance, forest type and disturbance level (degraded and overdegraded).

Aerial transects followed randomly stratified parallel lines. We used a small helicopter, type Bell 206 Jet Ranger, and followed the methodology developed in Sabah and described by Ancrenaz *et al*. (2005). Helicopter speed and height were constant at 70 km/hour and 60-80 meters above the forest canopy. The co-pilot recorded the exact location of the aircraft every 30 seconds with a GPS, and collected information on habitat types, signs of wildlife presence and human activities. Combining available historic logging information and direct observation from the aircraft, we distinguished six different habitat classes: 1. Active logging; 2. Highly degraded and recently logged forests (logging less than 2 years old, many logging roads, open canopy, no re-growth of pioneer species); 3. Degraded forests (logging activities more than two years old, signs of forest regeneration, open canopy); 4. Old logged forests (logging more than 10 years old, most places –especially old logging roads- are infested with *Macaranga spp.* or Rubiaceae trees, canopy typically closed but short); 5. Fair forest (primary forest or forest lightly logged long ago, closed and diverse canopy, presence of diverse and tall emergent trees); 6. Unsuitable orang-utan habitat (river, large open areas, etc). From the back seat, two observers looked for orang-utan nests from either side of the helicopter and relayed all sightings to a nest recorder seated between them. All visible nests were recorded in this manner and the nest recorder noted the number of nests detected by the observers per each 30-s period.

Calculations

Ground nest densities were analyzed following line-transect analysis guidelines and were computed using the software Distance 4.2 (Buckland *et al*., 1998). Transformation of nest density into an orang-utan density was achieved with the formula:

$$\hat{D}_{Ape} = \frac{\hat{D}_{nest}}{\hat{p} * \hat{r} * \hat{t}}$$

where $D_{\mathbf{nest}}$ is the estimated nest density, p the estimated proportion of nest builders, t the estimated nest decay rate, and r the estimated daily rate of nest production. We used the same parameters previously determined in Sabah, to allow for direct comparison of population trends. We also used a differential nest decay rate taking into account the species of trees used for nesting (Ancrenaz *et al*., 2004b).

Aerial indexes (number of nest per km of flight) were converted into nest and orang-utan density estimates with the model designed for Sabah and extensively described in Ancrenaz *et al*., 2005: $\hat{D}_0 = \exp[4.7297 + 0.9796 \log(AI_0)]$, $\hat{D}_0$ being the estimated orang-utan nest density and AI_0 the general aerial index ($AI_0 = (AI_{left}+AI_{right})/2$). A final confidence interval for the predicted orang-utan nest densities was achieved with $\frac{\hat{D}_0}{C}, \hat{D}_0 \times C$, where $C = \exp(0.6067 \times \sqrt{1 + v*})$ and $v* = 0.1908 - 0.2628 \times \log(AI_0) + 0.1132[\log(AI_0)]^2$. Further statistical analysis were computed with the software SPSS.

CHAPTER 3

Of pongo, palms, and perceptions – A multidisciplinary assessment of Bornean orang-utans in an oil palm context, Kinabatangan, Sabah, Borneo.

Ancrenaz, M., Oram, F., Ambu, L., Lackman, I., Ahmad, E., Elahan, H., Kler, H., Abram, N.K., Meijaard, E. 2014. *Oryx*.
Available on CJO2014. doi:10.1017/S0030605313001270

ABSTRACT

The oil palm industry is often blamed for the demise of iconic species such as the orangutan in Borneo. Since the oil palm industry is likely to continue to expand in the near future, orangutan conservation requires a better understanding of how the species could be accommodated in this human-transformed environment. Results from a combination of repeated ground transects, aerial presence/absence surveys, and interviews of workers in mature palm oil plantations of the lower Kinabatangan (eastern Sabah) provide an overall picture of the current situation of wild orangutans in an agro-industrial oil palm landscape. Our results show orangutans penetrate within mature plantations and use oil palm trees for nesting. The vast majority of oil palm workers report orangutans of all age-sex classes within the estates but fail to report any negative impact on productivity of mature palms. Our surveys also show that orangutan presence in the mature oil palm landscape of the Kinabatangan is highly correlated with proximity to natural forest patches. These results strongly suggest that forest patches, even fragmented and highly degraded, are required to sustain the species in human-transformed landscapes, and that homogenous oil palm plantations are incompatible with viable populations of orangutans. The cessation of further forest conversion to agriculture and the enforcement of better management practices could minimize the strong negative impacts of oil palm development on orangutan survival and better reconcile this industry with orangutan conservation.

INTRODUCTION

In Southeast Asia, conversion of forests to agriculture has reached unprecedented levels and is a major contributor to the current biodiversity extinction crisis (Sodhi *et al*., 2004). Orangutans (*Pongo* spp.) have become a focal point of conflict between economic development and environmental conservation. Today, the oil palm development is a major driver in the destruction of orangutan habitat (Gilbert, 2012; Wich *et al*., 2012a). This industry is also associated with continued killings of orangutans even though the Bornean (*P. pygmaeus*) and the Sumatran (*P. abelii*) orangutan are fully protected species in both Malaysia and Indonesia (Meijaard *et al*., 2011a). On the other hand, the economic benefits generated by this industry stimulate significant public and political support in these countries (Rist *et al*., 2010) and industrial expansion is likely to continue, at least for the next few decades (Miettinen *et al*., 2012).

Under current standard practice, industrial-scale agriculture has very limited compatibility with conservation of tropical wildlife (Koh & Wilcove, 2008). However, more and more studies report the presence of endangered and protected wildlife species in oil palm landscapes, such as the tiger (*Panthera tigris*) in Sumatra (Maddox *et al*., 2007) or the elephants (*Elephas maximus*) in Borneo (Estes *et al*., 2012). New thinking is needed to reconcile a healthy oil palm sector with biodiversity conservation and all stakeholders need to engage genuinely and positively to seek solutions rather than focusing on merely polarizing the debate (Meijaard *et al*., 2012).

Over the past fifteen years, the Kinabatangan Orangutan Conservation Programme (KOCP) from the French NGO HUTAN has studied the orangutan population living in the Kinabatangan River floodplain region (Eastern Sabah, Malaysia, Borneo) (Ancrenaz *et al*., 2004a; Ancrenaz *et al*., 2004b). Recent observations indicated that some orangutans were using the oil palm matrix in the area: sightings of nests in isolated patches of forest completely surrounded by oil palm plantations, sightings of animals within the estates, informal reports from oil palm workers. Based on this evidence, HUTAN and the Sabah Wildlife Department decided to conduct a general assessment of orangutan presence in the mature oil palm landscape of the Kinabatangan.

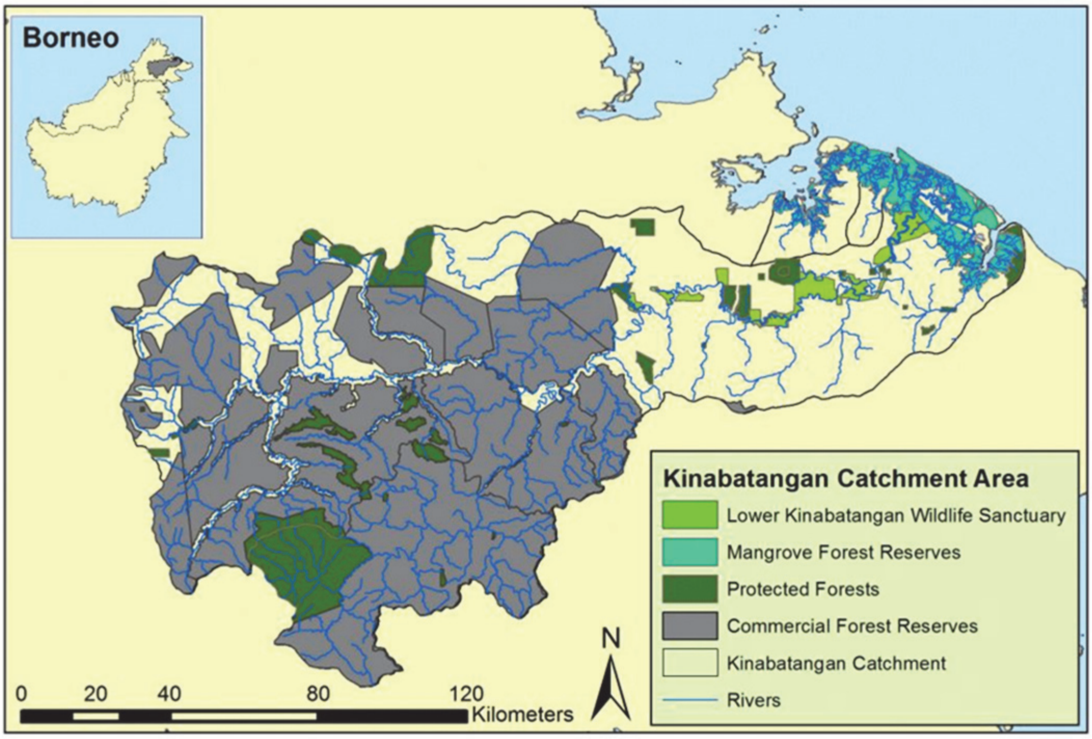
The major objectives of this assessment were to determine (1) if orangutan presence in mature plantations is localized or occurs throughout the entire lower Kinabatangan area; (2) if, when and how far the animals penetrate mature oil palm plantations; (3) if the animals use the palms for nesting, for food or for traveling; (4) the nest decay rate in oil palm plants; (5) if the animals are responsible for any type of damages to mature palms; (6) if plantation workers are aware of orangutans entering palm oil estates. To fulfill objectives 1 and 2 we used aerial surveys to determine the species' range through detection of their nests in the canopy following established methods (Ancrenaz *et al*., 2005). Objectives 1, 2, 3 and 4 were also investigated by regular ground monitoring of an oil palm estate bordered by natural forest. Interview surveys can produce reliable information about presence/absence as well as people’s tolerance of wildlife (Meijaard *et al*., 2011b). We therefore conducted a major interview survey of oil palm workers to better understand orangutan use of oil palm plantations. Results of these interview surveys will be presented in a stand-alone article, but some of the conclusions are presented here to document objectives 2, 5 and 6.

This study fits into a broader research initiative—the Borneo Futures —that assesses optimal land use options for Borneo Island and their macro-ecological, economic, and social impacts. Our ultimate goal is to use our findings to work with palm oil companies and relevant government agencies to develop and implement best management practices to enhance biodiversity support within the agro-industrial landscape and to reconcile industry practice with environmental commitments made by the Sabah Government (SWD 2012).

STUDY AREA

We conducted this research in the Lower Kinabatangan River floodplain, catchment area of 16,800 km^2 located in Eastern Sabah. Drastic changes have occurred since the onset of commercial logging in the early 1960s (Mc Morrow & Talip, 2001) and only about 750 km^2 (or 4% of the total watershed) of highly fragmented and degraded forests remain in the lower parts of Kinabatangan (Figure 3.1). About two-thirds of these lowland forests are currently protected, comprising the Lower Kinabatangan Wildlife Sanctuary (LKWS) and several Class I Virgin Jungle Forest Reserves. The major land use matrix outside these forest fragments is made up of extensive oil palm plantations, processing mills, roads, human settlements, small food crop farms, orchards and small patches of degraded forests under private or state ownership.

The HUTAN-KOCP team of local field research assistants is based in Sukau and has more than 15 years of continuous experience conducting orangutan surveys, behavioral study and interviews (Ancrenaz *et al*., 2004a).



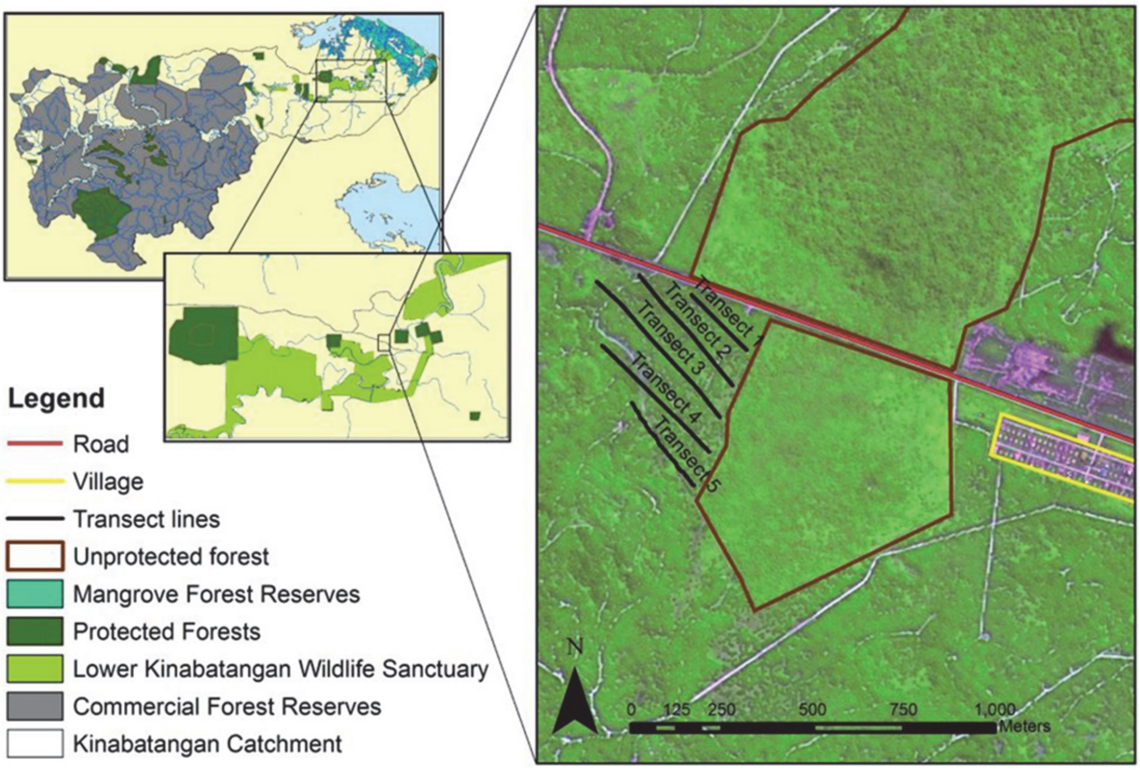
Map 3.1: Map showing the remaining forests in the Kinabatangan River basin (eastern Sabah, Malaysian Borneo).

METHODS

A team of four HUTAN experienced staff conducted two aerial surveys in June 2008 and September 2012 with a small helicopter (Bell 206) at low speed (around 60 knots) and low altitude (below 100 m above the canopy) following Ancrenaz *et al*. (2005). These flights aimed to record the location of small isolated patches of forest and to detect if orangutan nests were present in these patches. Forest patches were identified from satellite imagery, from ground surveys and during the flights. For every forest patch identified during the flights, we recorded the following information: 1. Location (GPS coordinates); 2. Approximate size of the patch in four classes: very small (less than five trees) – small (more than five trees and less than 1 ha) – medium (approximately more than 1 ha but less than 10 ha) – large size (more than 10 ha); 3. Degradation stage of the forest (by using a combination of visuals about canopy closeness, presence of large emergent trees, presence of invasive climbers, signs of human activities (following Ancrenaz *et al*., 2005); 4. Number of orangutan nests (six classes: none; single: 1

nest; very few: 1 to 5 nests; few: 5 to 10 nests; medium: 10 to 20 nests; many: more than 20 nests). Estimating nest abundance requires flying randomly located line transects above large contiguous forest areas (Ancrenaz *et al*., 2005). Because of the small size of the forest patches, it was impossible to derive abundance estimates from these surveys so we only assigned presence/absence.

Following several reports of orangutan sightings in an estate bordering a forest patch close to the village of PPMS-Sukau (95 houses, inhabited by about 600 people), we established five line-transects (length between 300 m and 800 m – total length of 2,850 m) within this oil palm estate. Inter-transect distance was about 500 m (Figure 3.2). From February 2011 to October 2012, the same team surveyed the five transects for signs of oil palm use by orangutans: every ten days between February and August 2011, (n=24 visits), then twice a month (n=22 visits: no visit was conducted in December 2011 and January 2012 because of the rainy season). For each survey, three lines of palms were assessed on both sides of the transect baseline. Since palms are planted at regular intervals of 10 m from each other, about 1,500 palms were assessed during every survey. Signs left by orangutans included nests and broken or bent leaves. Their location was recorded by GPS and photographed. As it was not possible to determine if a damage event was made by one orangutan or more, or in a single or a number of forays, damage results are descriptive rather than specifically quantifiable. Fifteen isolated non-palm trees (mostly *Acanthocephalus chinensis*) were standing close to the transects within the oil palm estate and were monitored.



Map 3.2: Map showing the five permanent line transects located in an oil palm estate close to the Sukau-PPMS village (adapted from a satellite image).

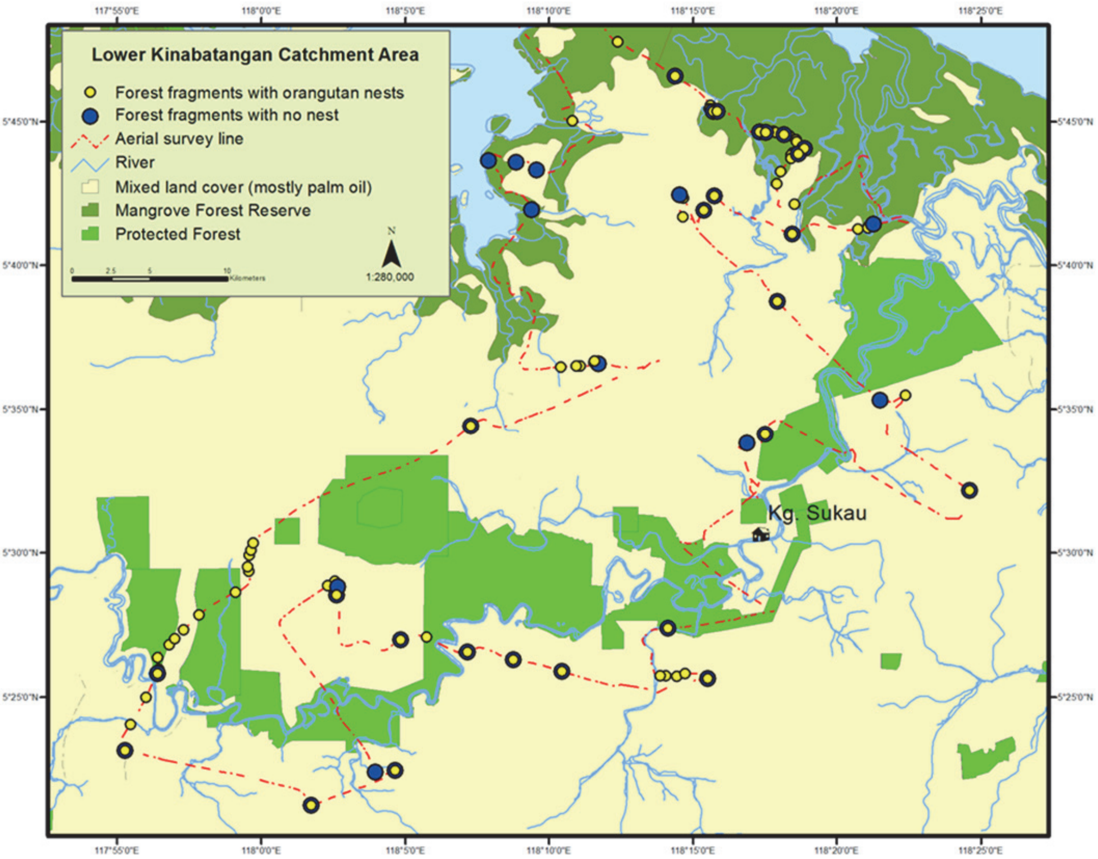
Orangutan nests in palm trees were monitored following Ancrenaz *et al*. (2004a) to determine their decay rate. A nest was included in our experiment only when we witnessed its construction (n=2) or when we detected a strong smell of urine or feces under the nest (n=10), indicating that it was not more than 1 or 2 nights old (Ancrenaz *et al*., 2004a). We conducting a separate experiment to assess the impact of nest building and leaf destruction on fruit productivity by selecting three oil palm trees with a minimum of five leaves recently damaged by orangutans for nesting or feeding. As a control, we included the five nearest palms without any orangutan damage (n=15). Once a month, we counted the number of fruit bundles hanging from the palms and that had been harvested (indicated by the number of cut stems visible on the palm). We then compared the results between damaged and non-damaged plants with a t-test using SPSS 14.0.

In September/November 2011 and June/July 2012, we conducted interview surveys to collect specific information about the use of oil palm plantations by orangutans and to document the general perception of oil palm workers about orangutans in lower Kinabatangan. The questionnaire was specifically targeted to oil palm plantation workers who spend most of their time within the oil palm landscape itself. The Sabah Wildlife Advisory Panel approved all content. A letter of consent issued by the Director of the Sabah Wildlife Department was presented to all estate managers, and an introductory text was read to all survey participants explaining the goals of the interviews. Anonymity of respondents was ensured to reduce the chance of biased results and the identity of respondents was not reported or shared with the plantation administration. A team of trained KOCP research assistants conducted the interviews and followed similar protocols and recommendations as Meijaard *et al*. (2011b).

The questionnaire comprised a mix of 48 open-ended and closed-single answer questions in Malay. Eleven questions established the basic demographics of the respondents (age, sex, type of work, country of origin, and how long they had lived in the area). Respondent's reliability was then assessed by presenting photographs of eight animals known to be found in the local plantation landscape. People who correctly identified orangutans were considered as "highly reliable". Only these interviews were used in the analysis; all others were discarded. Respondents were then asked a series of 23 questions about the specifics of the orangutan sightings (if any): location, time, number and description of individuals, activities, etc. Finally, we asked 11 questions on general perceptions about orangutan. We interviewed 560 plantation field workers from 12 commercial oil palm estates (average 2,500 ha planted each), three small holders and one village bordering a protected forest.

RESULTS

The 2008 aerial surveys revealed the presence of more than 100 orangutan nests in mangroves located between the sea and newly established plantations further inland (Figure 2.3), although mangroves are generally not considered as orangutan habitat (Rijksen & Meijaard 1999). Some of these nests were located in nipah palms (*Nypa fruticans*), while other nests were observed in taller trees (*Rhizophora sp*., *Brugiera sp*., *Intsia palembanica*). Further towards the interior, away from the mangrove area, we recorded 32 forest islands completely surrounded by oil palm plantations that contained orangutan nests (from one nest to about thirty, for a total of more than 120 nests). The size of each patch of "forest" ranged from 1 tree to less than 100 ha. During the flight, we saw that most of these forest patches were located on ground unsuitable for agriculture (limestone, steep slopes, quarries, swamps, etc.). All these forest patches were highly degraded, without a closed tree canopy, mostly covered with pioneer tree species and invaded by climbers and creepers. Some of these patches were located more than two km away from the nearest forest edge (with the most isolated patch with orangutan nest six km away from another forest patch). In 2012, during the second aerial survey, we recorded nests in most of the mangroves identified in 2008 except in the north-western part of the mangrove forest reserves that was recently converted to oil palm monoculture (Figure 2.3). From the 32 non-mangrove forest patches identified in 2008, only 15 patches were still standing in 2012, 14 patches had disappeared and had been converted to oil palm plantations and 3 patches were in the process of being converted. We identified about 60 nests in 11 of the remaining forest patches (or 75% of all forest patches identified during our flight).



Map 3.3: Map showing nests and forest patches identified during the 2012 aerial flight.

The 1,500 palms and 15 trees included in the regular ground monitoring were checked during 46 surveys throughout the study period. The estate owner cleared a broad area along the fence line and created a deep trench separating the estate from the forest in late July 2012. No orangutan sign was detected between August and November 2012 in this plantation, and only data collected before July 2012 were included in the final analysis (n=42 point checks). A total of 36 nests built by orangutans were recorded in palm trees (representing 0.06% of the total number of palms monitored during the 42 surveys) and four nests in non-palm trees (about 0.6%). Orangutans use the central part of the palm to build their nest, creating a platform of broken leaves to support the inner part of the nest, and bending leaves at the periphery. Bent leaves unfold after a few days or weeks depending on weather conditions (wind, rain) with no obvious coloration changes. Broken leaves however start to dry after a few weeks and can remain visible for several months in some cases (Plate 1). From the 36 nests built in oil palm trees, we included 12 new nests in the nest decay rate study. The average decay rate for these nests was 97.1 days (n=12, S.D.=52.1 days), with one outlier lasting up to 242 days. After removing the outlier, the average decay time became significantly shorter with 83.9 days (n=11, S.D.=26.0 days). The majority of nests were located close to the edge of a forest patch: average=62 m (S.D.=41 m), and the largest distance was only 150 m. Leaves broken or damaged by orangutan because of traveling or feeding activities were recorded in 41 additional palms (0.065% of our total sample size). These damages were recorded up to 400 m away from a forest edge. Appearance time of new nests and damages to palms was highly correlated (Pearson value=0.835; p<0.001). Most damages and nests occurred between the first months of the year but failed to show any significant temporal differences (t-test comparing the number of events in February-June vs July-November: t-test: t=1.52; df=10.27; p=0.159). A t-test comparing the average of fruit bundles produced by damaged trees (n=42; mean=6.6; S.E.=0.38; 95% Confidence Interval=5.82-7.37) and non-damaged trees (n=210; mean=7.33; S.E.=0.245; 95% CI=6.84-7.83) failed to show a statistically significant difference between the two samples: F=0.562; t value=0.311; p=0.757.

Plate 1: Picture of a nest built by an orangutan in a mature palm tree.

Detailed quantitative and qualitative results of the interview surveys will be presented in a separate article. We present here some preliminary data as the percentage of respondents that gave a particular response to describe the orangutan status within the oil palm landscape of Kinabatangan. Out of a total of 560 interviewed people, 214 reported seeing an orangutan at least once. Of these 214 respondents, 156 (27.8% of the general total) were scored as highly reliable. Out of these 156 respondents, 141 people (90.3%) reported having seen an orangutan within the local oil palm plantation or immediate border areas at least once over the past few years. The average age of these 141 respondents was 31.4 years (S.D.=10.3) and two-thirds were males (n=90). Ninety-two informants (65.2%) reported an orangutan sighting within the last two years, and 103 (73%) within the last three years, showing that most of these sightings were relatively recent. The majority of reliable respondents (81 persons – 57.4%) reported seeing an orangutan within non-oil palm forest patches but less than 20 m from the plantations while forty two respondents (29.8%) reported sightings of orangutan within homogenous oil palms away from the forest. The furthest sighting was about 5 km from the nearest forest patch. Two respondents reported the sighting of orangutans crossing the main paved road leading to Sukau (one flanged male and one adult of undetermined sex). Of the 42 respondents who reported seeing orangutans within the monoculture oil palms, 17 (40 %) reported sightings of animals in oil palm trees with the remainder being of animals walking or running on the ground. Although several questions intended to determine the sex-age classes of orangutans it was extremely difficult to come up with clear conclusions. Exceptions were one report of a non-flanged individual moving on its own; twelve reports of adult females with a clinging baby; three of an adult female with an accompanying juvenile, and 14 of a flanged male. These reports indicate that all sex-age classes could be seen within this landscape. When asked if workers were aware of any problems or conflicts with orangutans, 97 respondents (68.8 %) said that orangutans caused “no disturbance” in mature palm trees except for breaking leaves but this was considered of little or no consequence to palm productivity, reinforcing the findings of our own experiment. We collected only two reliable reports of a flanged adult male orangutan consuming oil palm fruits that have dropped from the bunches left on the ground after harvest.

DISCUSSION

Our aerial and ground surveys show that orangutan nests are found throughout the entire oil palm matrix of lower Kinabatangan: in small forest patches and isolated trees, but more surprisingly in palms and in mangrove forests. These unexpected findings are strongly reinforced by the relatively high encounter rate between oil palm workers and orangutans within the agro-industrial landscape. The frequent use by orangutans of a mature oil palm matrix has not been previously recognized in the scientific literature (but see Campbell-Smith *et al.*, 2011a for an exception), and needs further investigation.

Our results suggest that the destruction of leaves by orangutans in mature palms (for nesting, locomotion or feeding) has no consequence on the fruit productivity of the plant. This contrasts with the high rate of orangutan damages recorded in young palms under 4-5 years of age (Yuwono *et al*.; 2007). Our regular ground monitoring suggests that orangutans preferentially select non-oil palm trees for nesting within a plantation, but also shows that palm trees are used for nesting. Nests built in oil palms are very similar in form and shape to the nests built by orangutans in nipah palms in mangrove areas (MA, pers. obs.) or by chimpanzees in native wild oil palm trees in Guinea Bissau (Sousa *et al*., 2011). The nest decay rate in a palm is short compared to other tree species (Ancrenaz *et al*., 2004a).

Up to 90% of orangutan signs identified within oil palm (nests, broken leaves) were found less than 50 m away from forest patches, suggesting that orangutan distribution within an oil palm estate depends primarily on the presence of forests and non-palm trees. Unless non-palm trees are present, the penetration of homogenous stands of oil palms appears relatively weak. However leaves broken by orangutans were recorded more than 500 m from a forest twice, and a precise mapping of the industrial landscape of Kinabatangan revealed that orangutans can cross at least 5 km of pure mature oil palm stands to disperse between isolated forest patches. Interviews also indicate that males disperse further in an oil palm landscape than females, as already shown in Sumatra (Campbell-Smith *et al*., 2011a; Campbell-Smith *et al*., 2011b). However, unlike in Sumatra, our results show that females and young are also detected by oil palm workers in the plantations. Although orangutans can brachiate between palms, they often walk on the ground to move throughout an oil palm field, to cross roads and open areas or to move quickly when disturbed by people. An increased terrestrial locomotion in a human-made matrix that is extensively used by people and domestic stock increases the risks of zoonoses and anthropozoonoses transmission: assessing the health status and sanitary risks of animals that are using agro-industrial landscapes should therefore be a priority (Woolhouse & Gaunt, 2009).

The percentage of reliable respondents who reported sightings in the oil palm plantation landscape (90.2 %) is much higher that the percentage of villagers who reported having seen wild orangutans in the forests of Kalimantan during a general interview study (42%) (Meijaard *et al*., 2011a; Meijaard *et al*., 2011b). The difference is probably due to the high density of people working in oil palm and the openness of oil palm areas compared to natural forest. But this may not fully explain why so many orangutans are reported in oil palm plantations in Kinabatangan. We therefore hypothesize that orangutan abundance in this oil palm landscape is significantly higher than so far acknowledged by the industry and scientists.

Information generated through our study contributes to a general picture of the use of large industrial oil palm plantations by orangutans in Kinabatangan, from which it becomes possible to derive generic recommendations for better management of the oil palm landscape. Recent studies have demonstrated that the orangutan species is more resilient to habitat changes than was originally thought: viable orangutan populations are found in commercial forest reserves exploited for timber using reduced-impact logging practices in Sabah (Ancrenaz *et al*., 2010); significant numbers of individuals are found in acacia plantations in Eastern Kalimantan (Meijaard *et al*., 2010); and stable groups have been living in a mosaic of mixed agriculture and forest for more than 20 years in Sumatra (Campbell-Smith *et al*., 2011b). However, orangutan survival in these highly modified landscapes is intimately related to human tolerance towards them (Wich *et al*., 2012). Indeed, hunting remains a major driver of orangutan extinction and will invariably wipe out these populations if animals are killed to mitigate conflicts or for any other reasons (Marshall *et al*., 2009). Although our current results show that orangutans can use the agro-industrial oil palm matrix in Kinabatangan, this does not suggest that orangutans can survive in monoculture oil palm plantations. Indeed, most direct and indirect sightings of orangutans reported in oil palm plantations were close to a forest edge, indicating that their survival is reliant on the presence of non-palm trees and patches of natural forest in the landscape. In the early 1960s the lower Kinabatangan floodplain was covered with forests and the overall orangutan density was estimated to 1 individual per square mile (Yoshiba 1964). Although this estimate is extremely conservative and may be well below the original orangutan abundance in these forests, such a value would mean that over 5,000 orangutans were found in the forests of the lower Kinabatangan (about 8,000 km^2) before their conversion to agriculture. Today, our latest estimates for lower Kinabatangan are about 1,000 individuals (Ancrenaz et al., 2004b), and recent genetic analysis showed that this population has declined by more than 95% in the last 100 years (Goossens *et al*., 2006b). These data show that converting forests occupied by orangutans to oil palm plantations has a devastating impact on orangutan survival. When forests are converted to large scale agriculture like oil palm plantations, the majority of the resident orangutans are either killed outright (Wich *et al*., 2012a) or likely starve as neither young oil palm shoots nor mature oil palm can provide a sufficient food source for the largest arboreal mammal.

CONCLUSIONS AND RECOMMENDATIONS

Many relevant recommendations to minimize the strong negative impacts of oil palm development on orangutan survival are already captured in broader guidelines for sustainable oil palm management (RSPO 2007). We reiterate the most important ones with regard to orangutan conservation in an oil palm context (Dennis *et al*., 2010), and add specific recommendations based on our latest findings.

- The value of patches of over-degraded forest for orangutan conservation must be recognized and acknowledged by government planners and policy makers, the scientific community, the private sector and all other land-users;
- Before any new development, it must be ensured that forest patches and corridors are identified, marked and set aside. Although some studies showed that a spatial juxtaposition of forest fragments in the oil palm landscape had little effect on the patterns of bird diversity (Edwards *et al*., 2010), it is commonly recognized that retaining forests within an agro-industrial landscape is key to maintaining ecosystem functionality and meta-populations of many wildlife species (Koh 2008; McShea *et al*., 2009);
- For landscapes that have already been developed (such as eastern Sabah), it is necessary to precisely identify all remaining patches of forest (irrespective of their size or degradation stage) formally on paper and physically on the ground. These patches should not be converted but incorporated in land use plans as ecological set asides, and appropriately managed. These patches could also act as refuges for predators that will control pest species in the plantations (Koh 2008);
- Planting non-palm trees throughout an agro-industrial oil palm landscape will increase food opportunities for wildlife or possible nesting sites for orangutans. In mature oil palm this would boost orangutan survival without negatively impacting palm oil production;
- Trenches and stripes of bare lands seem to deter orangutans from entering oil palm plantations. This method could physically separate plantations from forests inhabited by orangutans to mitigate conflicts when plantations are newly established. When palms become older and mature, these trenches could be bridged to allow orangutans to move across the mature oil palm landscape;
- All sightings of orangutans and other protected wildlife need to be reported by oil palm workers to their team leaders and a proper flow of information needs to be established between field operation management and wildlife authorities;
- A zero-tolerance for orangutan killing needs to be strictly enforced by all management levels of a company.

To conclude, we need a shift in focus from conserving site and species to respecting landscapes and processes and to envision a larger scale landscape approach (Laurance *et al*., 2012). This can be achieved only if scientists, NGOs, government agencies and the private sector genuinely engage and work closely together with consumers to identify innovative solutions that will address the needs to develop more sustainable practices (Bateman *et al*., 2012, Meijaard *et al*., 2011c).

CHAPTER 4:

Coming down from the trees: Is terrestrial activity in Bornean orang-utans natural or disturbance driven?

Ancrenaz, M., Sollmann, R., Meijaard, E., Hearn, A.J., Ross, J., Samejima, H., Loken, B., Cheyne, S.M., Stark, D.J., Gardner, P.C., Goossens, B., Mohamed, A., Bohm, T., Matsuda, I., Nakabayasi, M., Lee, S.K., Bernard, H., Brodie, J., Wich, S., Fredriksson, G., Hanya, G., Harrison, M.E., Kanamori, T., Petra Kretzschmar, David W. Macdonald, Peter Riger, Stephanie Spehar, Ambu, L.N., Wilting, A. 2014. *Nature Scientific Report,* 4: 4024.

DOI: 10.1038/srep04024 (2014).

ABSTRACT

The orangutan is the world's largest arboreal mammal, and images of the red ape moving through the tropical forest canopy symbolise its typical arboreal behaviour. Records of terrestrial behaviour are scarce and often associated with habitat disturbance. We conducted a large-scale species-level analysis of ground-based camera-trapping data to evaluate the extent to which Bornean orangutans *Pongo pygmaeus* come down from the trees to travel terrestrially, and whether they are indeed forced to the ground primarily by anthropogenic forest disturbances. Although the degree of forest disturbance and canopy gap size influenced terrestriality, orangutans were recorded on the ground as frequently in heavily degraded habitats as in primary forests. Furthermore, all age-sex classes were recorded on the ground (flanged males more often). This suggests that terrestrial locomotion is part of the Bornean orangutan's natural behavioural repertoire to a much greater extent than previously thought, and is only modified by habitat disturbance. The capacity of orangutans to come down from the trees may increase their ability to cope with at least smaller-scale forest fragmentation, and to cross moderately open spaces in mosaic landscapes, although the extent of this versatility remains to be investigated.

INTRODUCTION

The Bornean orangutan *Pongo pygmaeus* is the largest arboreal species in the world and its survival is linked to forest habitat (Delgado & Van Schaik, 2000; Mac Kinnon, 1974). Despite the orangutan's iconic value and millions of dollars spent annually on its conservation (Meijaard *et al*., 2011c), the species is declining throughout its range. In Borneo, more than 70% of orangutans occur in fragmented multiple-use and human-modified forests that have lost many of their original ecological characteristics (Ancrenaz *et al*., 2005; Wich *et al*., 2012). The consequences of these drastic habitat changes on orangutan survival, behaviour and ecology are only just starting to be documented (Meijaard *et al*., 2009; Ancrenaz *et al*., 2010; Meijaard *et al*., 2011; Wich *et al*., 2012). Some authors have proposed that forest degradation may force the species to the ground more frequently (Rijksen & Meijaard, 1999; Loken *et al*., 2013). We can suppose that increased terrestriality would increase predation risk, interactions with and persecution by humans, and exposure to novel pathogens. On the other hand, terrestrial behaviour could also facilitate movement and, therefore, dispersal, especially in degraded or fragmented landscapes as a result of natural or man-made processes. It could also create new opportunities to access different food sources (Ancrenaz *et al*., 2014). Ultimately, a better understanding of the drivers of orangutan terrestriality and how this influences dispersal and movement is important for designing effective landscape management strategies for maintaining viable meta-populations of this species in Borneo (Wich *et al*., 2012a).

Most studies of orangutan locomotion have been based on direct observations (Thorpe *et al*., 2007; Thorpe & Crompton, 2009). However, orangutans may be reluctant to come to the ground in the presence of human observers and remote camera traps present an opportunity to overcome this potential bias (Loken *et al*., 2013). We conducted a large-scale species-level analysis of ground-based camera-trapping data to evaluate the extent to which Bornean orangutans travel terrestrially and to investigate possible drivers for this behaviour.

RESULTS

Altogether we collected camera-trapping data from 16 study areas 103 from Sabah (Malaysia) and East and Central Kalimantan (both Indonesia), for which reliable orangutan density estimates were available (Table 4.1). Pictures were collected between June 2006 and March 2013, and included data from all months of the year. The total dataset encompassed 159,152 trap days at 1,409 independent camera-trap stations. Orangutans were recorded on the ground in all forest classes, indicating that terrestrial activity occurs regardless of habitat disturbance. Nevertheless, the regression model revealed that forest class, camera-trap placement and orangutan density influenced the photographic frequency and the probability of orangutans coming to the ground (Table 4.3, Figure 4.1 A-C). Photographic frequencies were significantly higher beneath large canopy gaps than under closed canopy (Figure 4.1A & 4.1B, Table 4.3). In 428 out of 641 orangutan records the sex-age class could be reliably determined (see Methods). We observed females alone 27 times, females with clinging babies or with walking young 63 and 25 times, respectively, unflanged males 48 times, and flanged males 265 times. We recorded flanged males significantly more often than expected based on their proportion in the population (see Methods) ($\chi^2 = 32.050$, df = 1, $p < 0.001$), suggesting they are more terrestrial than unflanged males, and females. Only 15 orangutan records were obtained during night time (before 0600h and after 1800h).

Table 4.1: Summary statistics for orangutan camera trapping data from Borneo used in the present analysis.

No	Study site	Status[1]	State	No of stations	No of trap nights	No of records	Forest class	Orangutan density [ind / km²]	Density reference
1	Bawan Forest	CFR	Central Kalimantan, Indonesia	65	2,064	2	REC-RIL	2.15	Harrisson *et al.*, 2012
2	Croker Range Park	NP	Sabah, Malaysia	35	3,999	0	PRIM & VOL	1.0	Ancrenaz *et al.*, 2005
3	Danum Valley Conservation Area	TPA	Sabah, Malaysia	198	20,223	51	PRIM	1.0	Ancrenaz *et al.*, 2005
4	Deramakot Forest Reserve	CFR	Sabah, Malaysia	144	10,532	25	VOL & OLD-RIL	1.5	Ancrenaz *et al.*, 2005
5	Lower Kinabatangan Wildlife Sanctuary	WS	Sabah, Malaysia	128	19,602	179	VOL	1.1 - 3.9[2]	Ancrenaz *et al.*, 2004
6	Kuamut Forest Reserve	CFR	Sabah, Malaysia	38	1,949	2	REC-CL	0.1 - 1.4[2]	Ancrenaz *et al.*, 2005
7	Kutai National Park	NP	East Kalimantan, Indonesia	53	3,310	42	VOL	1.0 - 1.3[2]	Spehar, pers. com.
8	Maliau Basin	TPA	Sabah, Malaysia	27	5,232	0	PRIM & OLD-REC	0.1	Ancrenaz *et al.*, 2005
9	Malua Forest Reserve	CFR	Sabah, Malaysia	107	9,730	40	REC-CL	1.3 - 1.6[2]	Ancrenaz *et al.*, 2005
10	Sabangau Peat Swamp Forest	NP	Central Kalimantan,	58	26,722	49	OLD-RIL	1.7	Ancrenaz *et al.*, 2007

			Indonesia						
11	Segaliud Lokan Forest Reserve	CFR	Sabah, Malaysia	67	3,452	19	OLD-CL & REC-RIL	1.2	Ancrenaz *et al.*, 2005
12	Kulamba Wildlife Reserve	WR	Sabah, Malaysia	4	252	2	VOL	2.3	Ancrenaz *et al.*, 2005
13	Tabin Wildlife Reserve	WR	Sabah, Malaysia	283	28,462	104	VOL	1.3	Ancrenaz *et al.*, 2005
14	Tangkulap Forest Reserve	CFR	Sabah, Malaysia	100	6,057	37	OLD-CL	0.6	Ancrenaz *et al.*, 2005
15	Ulu Segama Forest Reserve	CFR	Sabah, Malaysia	61	9,829	13	OLD-CL	1.1 - 1.4[2]	Ancrenaz *et al.*, 2010
16	Wehea Forest	CFR	East Kalimantan, Indonesia	41	7,737	76	OLD-RIL	1.1	Loken, pers. com.
	TOTAL			**1,409**	**159,152**	**641**			

[1] CFR = Commercial Forest Reserve; NP = National Park; TPA = Totally Protected Area; WS = Wildlife Sanctuary; WR = Wildlife Reserve; [2] Density varied between areas

Table 4.2: AIC summaries for zero-inflated Poisson regression of photo-counts of orangutans; models for the probability of coming to the ground as a function of forest class (for), camera trap placement (cam) and orangutan density (dens), conditional on best photographic frequency model containing all covariates.

Model	No. parameters	AIC	delta AIC	AIC weight
for + dens	16	2550.120	0.000	0.533
for + cam + dens	18	2550.783	0.664	0.364
cam + dens	13	2554.802	4.683	0.055
For	15	2555.798	5.678	0.032
hab + cam	17	2557.085	6.965	0.016
Dens	11	2565.759	15.640	0.000
Cam	12	2567.900	17.781	0.000
0	10	2573.684	23.565	0.000

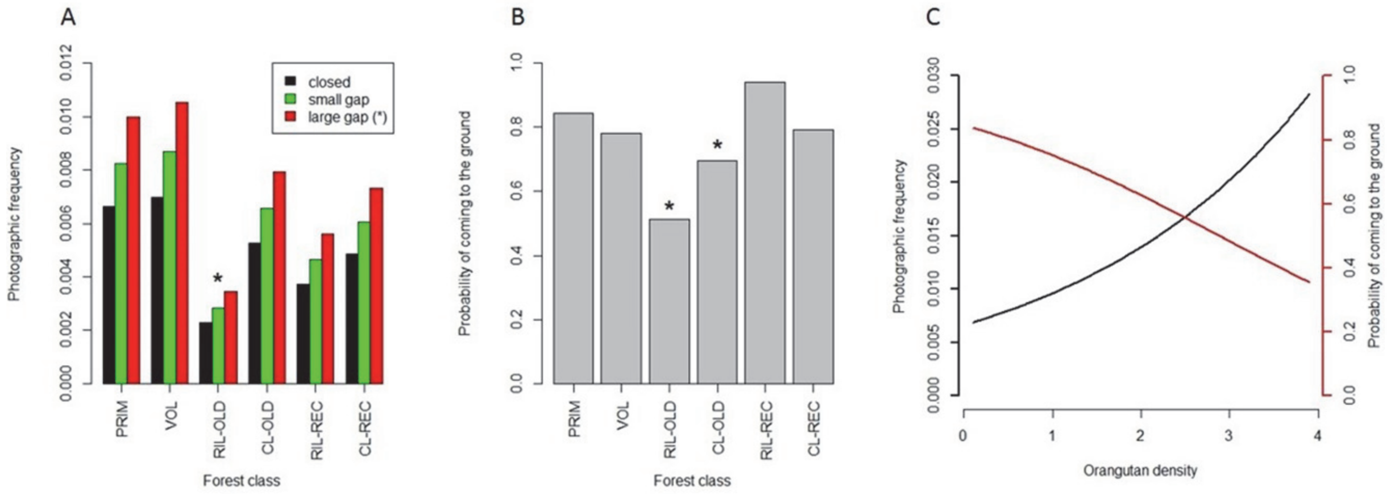


Figure 4.1: (A) Photographic frequency (including different camera-trap placement categories) and (B) probability of orangutans coming to the ground for six different forest classes ordered from primary to recently heavily logged forest (PRIM 5 primary forest; VOL 5 very old conventionally logged forest .20 years ago; RIL-OLD 5 reduced impact logging 2–20 years ago; CL-old 5 conventional logging 2–20 years ago; RIL-REC 5 reduced impact logging within the last 2 years; RIL-REC 5 conventional logging in the last 2 years). (C) Relationship of photographic frequency (black) and probability of orangutans coming to the ground (red) with orangutan density, plotted for primary forest, but patterns for other forest classes are equivalent.

Table 4.3: Model-averaged parameter estimates from zero-inflated Poisson regression of photographic frequencies of orangutans against forest class (PRIM, VOL, RIL-OLD, CL-OLD, RIL-REC, CL-REC, see Figure 1 for abbreviations), camera trap placement (closed canopy, small gap, large gap) and orangutan density. Primary forest and closed canopy were reference categories in the regression.

Parameter	Coefficients	Estimate	SE	Lower CI	Upper CI	z value	p value
Frequency (log scale)	Intercept	-5.017	0.227	-5.462	-4.572	22.098	< 0.001
	β (VOL)	0.053	0.242	-0.423	0.528	0.217	0.828
	β (RIL-OLD)	-1.064	0.300	-1.653	-0.475	3.542	< 0.001
	β (CL-OLD)	-0.229	0.302	-0.821	0.363	0.758	0.448
	β (RIL-REC)	-0.578	1.165	-2.862	1.706	0.496	0.620
	β (CL-REC)	-0.313	0.332	-0.963	0.337	0.943	0.346
	β (small gap)	0.220	0.152	-0.079	0.518	1.443	0.149
	β (large gap)	0.412	0.179	0.061	0.762	2.300	0.021
	β (density)	0.372	0.106	0.166	0.579	3.529	< 0.001
Probability (logit scale)	Intercept	1.694	0.337	1.033	2.355	5.022	< 0.001
	β (VOL)	-0.423	0.330	-1.070	0.224	1.283	0.200
	β (RIL-OLD)	-1.643	0.456	-2.537	-0.749	3.603	< 0.001
	β (CL-OLD)	-0.871	0.380	-1.615	-0.127	2.294	0.022
	β (RIL-REC)	1.070	1.420	-1.714	3.854	0.754	0.451
	β (CL-REC)	-0.353	0.456	-1.247	0.542	0.773	0.439
	β (small gap)	-0.461	0.300	-1.050	0.127	1.538	0.124
	β (large gap)	-0.025	0.398	-0.805	0.756	0.062	0.951
	β (density)	-0.587	0.217	-1.013	-0.162	2.706	0.007

DISCUSSION

Overall, Bornean orangutan terrestrial activity appears more common than previous anecdotal observations suggested (Loken *et al*., 2013), which indicates that the species exhibits a flexible and varied repertoire of locomotion. This is supported evolutionarily: the potential ancestors and fossil relative taxa of *Pongo*, are thought to have used more ground locomotion than the current *Pongo* (Begun & Kivell, 2011; Harrison & Chivers, 2006). This, in turn, has led to the suggestion that ancestral orangutans may have been able to cover larger distances on the ground (von Koenigswald 1986; Wich *et al*., 2009). It should be noted that the data used in the present analysis come predominantly from the subspecies *P. pygmaeus morio* in northeastern Borneo and there is the potential for regional differences in the species' response to forest characteristics driven by differences in ecological circumstances (Wich *et al*., 2009). For example, an analysis of raw model residuals by study site (Supplementary Information) showed stronger negative outliers for photographic counts from the Sabangau peat swamp (i.e., subspecies *P. p. wurmbi*) than from other sites, suggesting that swamp habitat may reduce terrestriality in orangutans. Further, preliminary data indicate that the Sumatran orangutan *Pongo abelii* is much less terrestrial, possibly because of the presence of tigers *Panthera tigris* as potential predators, which are absent from Borneo (Delgado & van Schaick, 2000).

Our analysis shows that the degree of terrestriality is modulated by forest structure. This suggests that anthropogenic canopy disruptions will increase terrestrial activity in orangutans, but habitat disturbance is not the only driver for this behaviour. Indeed, both photographic frequencies and probabilities of coming to the ground were lowest in areas logged by reduced impact logging schemes between two and 20 years ago and not, as expected if terrestriality were determined by disturbance, in primary forests. This may be caused by a continuous lower canopy layer that develops after reduced impact logging and is relatively easy to travel through without coming to the ground to cross gaps. In contrast, the irregular canopy structure in primary forests and the large man-made gaps in forests recently logged using conventional logging methods may increase the energetic costs of arboreal locomotion (Thorpe *et al*., 2007), offering an explanation for similar terrestriality in these forest classes. Although our data also support the perception that terrestriality in orangutans is most prevalent in larger and heavier flanged males (Rijksen & Meijaard, 1999), our camera trap data showed that all age-sex classes travel on the ground irrespective of habitat type. The ability to cross forest gaps, especially for males, which are the dispersing sex (Nater *et al*., 2011; Arora *et al*., 2012; Nietlisbach *et al*., 2012) suggests that gene flow can occur even in disturbed and possibly fragmented habitats (Ancrenaz *et al*., 2014a). In addition to occasional advantages in travelling from place to place, terrestriality could enhance the possibilities for foraging for terrestrial resources, such as succulent shoots, termites or mineral clay (Matsubayashi *et al*., 2011; Ancrenaz *et al*., 2014a). This may be particularly important during periods of habitat-wide fruit scarcity. Heightened orangutan terrestriality in human-modified landscapes and the resulting increase in contact with people creates new risks, such as increased susceptibility to hunting and exposure to new diseases, as great apes are vulnerable to many human diseases (Muehlenbein & Ancrenaz, 2009; Ryan and Walsh, 2011).

Our findings reinforce the importance of incorporating degraded forests recovering from logging disturbance into orangutan conservation strategies (Ancrenaz *et al*., 2010; Meijaard *et al*., 2011c; Wich *et al*., 2012a). The capacity of orangutans to come down from the trees may increase their ability to cope with at least smaller scale fragmentation (Ancrenaz *et al*., 2010), and to cross moderately open spaces in mosaic landscapes, although the extent of this versatility remains to be investigated. In order to design conservation management strategies that will allow for the species to persist in anthropogenic landscapes, however, practitioners need to be mindful of the potential risks associated with terrestrial activities in orangutans. The "man of the forest" cannot be regarded as safely tucked away up in the trees.

METHODS

Our analysis is a compilation of existing ground-based camera trapping data that had been collected at 16 sites in Borneo, mostly on the northern part of the island (Table 4.1).

Data base

To avoid inflated counts caused by repeated detections of the same individual, only one record per hour per camera site was included in the data analysis. We excluded all cameras that were placed at salt licks, and data from the orangutan rehabilitation site at Sepilok Forest Reserve, as we assumed that both factors could influence terrestrial behavior (i.e., a particular resource for the former (Matsubayashi *et al*., 2011) and habituation to humans for the latter (Russon, 2009).

To avoid spatial autocorrelation in the data, we only included camera-trap stations that were a minimum of 1 km apart from each other, assuming that orangutans do not move continuously along the ground over distances in the order of a kilometre (Ancrenaz *et al*., 2014b), so that events to come to the ground are independent at that scale. The independence of these observations would be compromised if orangutans routinely moved along the ground over 1 km. This assumption is backed by the observation that the *overall* (i.e. arboreal and terrestrial) maximum distance moved by orangutans within a day is in most cases below 1 km (Singleton et al., 2009). Considering these restrictions all analyses are based on 641 independent orangutan records taken at 1,409 stations during 159,152 trap days (see Table 4.1).

Analysis

All analyses were performed in R, version 2.15.1 (R, 2012).

- **Terrestrial activity as a function of forest disturbance and density**

We hypothesised that regional forest structure and camera-trap site specific canopy structure (also referred to as camera-trap placement), as well as orangutan density, could influence how often orangutans are photographed on the ground. We therefore classified forests into six classes, based on their current and past management history: 1. primary forest (PRIM; not disturbed); 2. very old conventionally logged forest (VOL; last logging more than 20 years ago); 3. old slightly logged forest (OLD-RIL; exploitation using reduced impact logging RIL) practices between 2-20 years ago); 4. old heavily logged forest (OLD-CL; conventional logging practices 2-20 years ago); 5. recent slightly logged forest (REC-RIL; RIL within the last 2 years); 6. recent heavily logged forest (REC-CL; conventional logging in the last 2 years). We further categorized camera trap placement according to Loken *et al.* (2013) as under closed canopy (0-3m gaps that orangutans are likely able to cross by tree swaying), small canopy gap (3-5m gaps that orang-utans might be able to cross by tree swaying), or large canopy gap (> 5m gaps that orang-utans are unlikely to cross by tree swaying). Gap size was determined post hoc based on field notes and photographs. We recognize that there might be some inherent error in classifying gap size post hoc, but the coarse classification of gap size should buffer most of that error. Orangutan densities were obtained from the literature and from unpublished data of the authors for each site (Table 1). We acknowledge that density estimates were obtained with different methods and that some of these methods are controversial: however, the estimates used here represent the best currently available data for these sites and are widely used to assess the status of the species. To quantify the influence of the above variables on orangutan terrestriality, we compiled the number of orangutan records taken at each camera location and analysed the data using a zero-inflated Poisson (ZIP) regression (Gelman and Hill, 2006). A ZIP model allows for over dispersion in counts in the form of excess zeros, which we observed in our data set. It is a Binomial-Poisson mixture that attempts to separate zero count into structural zeros (sites where orangutans never come to the ground so that we can only observe a zero count) and sampling zeros (sites where orangutans do come to the ground but we happen to not record them there). The binomial component of the ZIP model estimates the ***probability of coming to the ground*** at a given camera trap station. The Poisson component of the ZIP model describes the number of records we expect to observe (referred to as the ***photographic frequency***) at a camera trap, conditional on the species coming to the ground at all. Both parameters can be modelled as functions of covariates on the logit and log scale, respectively. We used station-specific survey effort (i.e., camera-trap days) as offset, and orangutan density, forest class, and camera-trap placement (characterised by station-specific canopy gap size) as model covariates.

We built a number of models, differing in the combination of explanatory covariates (forest class, canopy gap size and orangutan density), and used the Akaike Information Criterion (AIC) to select the most parsimonious ('best') model. Because we expect a direct relationship between the sampling effort at a camera-trap station and the number of pictures obtained, all models used the number of camera trap days each station was surveyed as an offset in the model for frequency. To reduce the total number of candidate models, we first explored different models for the photographic frequency while holding the probability of coming to the ground constant (i.e. no explanatory variables of the probability of coming to the ground). Conditional on the best frequency model we then built candidate 233 models for the probability of coming to the ground (Table 4.2). The best model for photographic frequency contained all three covariates. Conditional on this frequency model, the best overall model additionally contained effects of forest class and density on the probability of coming to the ground. The second-best model, which also included camera placement as a covariate on the probability of coming to the ground, only had a delta AIC relative to the best model of 0.66 and was therefore essentially equally supported by the data (Table 2). Since we were unable to determine a single best model, we employed model averaging, where parameter estimates are obtained as a weighted average over all candidate models (Burnham and Anderson, 2002).

- **Age-sex classes on the ground**

To investigate whether terrestrial behaviour is exhibited by all demographic classes (i.e. flanged males, unflanged males, females and females with offspring) we would have ideally run separate ZIP regressions for different classes, but identification of these classes was only possible with high certainty in about 50% of all camera trap records. We cannot assume that failure to identify the age-sex class occurs at random – it is much harder to distinguish a small male from a female, or ascertain that a female is with offspring, than it is to unambiguously identify a flanged male. The only analysis we conducted with respect to demographic class was, therefore, a comparison of the number of observed versus expected number of flanged male pictures using a Chi-square test. We expect a 50:50 male-female ratio in the orangutan population (Marshall *et al.*, 2009); within the males, on Borneo there are typically 1.6:1 flanged to unflanged males (Marshall *et al.*, 2009; Bruford *et al.*, 2010). Thus, if all demographic groups came to the ground relative to their occurrence in the population, we would expect flanged male pictures to comprise 31% of our total sample. We considered all pictures in which the demographic group could not be identified as “not flanged male” – this is unlikely to be true since pictures that only show small part of an orangutan could be of a flanged male. However, this procedure guaranteed a conservative approach towards the question of whether flanged males come to the ground more frequently than expected.

CHAPTER 5

Minimizing pathogen transmission at primate ecotourism destinations : the need for input from travel medicine

Muehlenbein, M.P. & Ancrenaz, M. 2009. *Journal of Travel Medicine*, 16 (4): 229-232.

DOI: 10.1111/j.1708-8305.2009.00346.x

EDITORIAL

Tourism generates more than 9% of the global gross domestic product and may account for almost half of the gross domestic product in developing countries with biodiversity-rich areas (WTTC, 2009; WTO, 2004). Nature-based tourism accounts for a growing proportion of international tourism activity. Ecotourism is a sustainable version of nature tourism with the following components:

- Contributes to conservation of biodiversity;
- Sustains the wellbeing of local people;
- Includes an interpretation/learning experience;
- Involves responsible action on the part of tourists and the tourism industry;
- Is delivered primarily to small groups by small-scale businesses;
- Requires lowest possible consumption of nonrenewable resources;
- Stresses local participation, ownership and business opportunities, particularly for rural people (Epler Wood, 2002).

Ecotourism accounts for a significant proportion of all international tourism, and revenue generated by these activities could enhance economic opportunities for local residents, support environmental education, and protect the natural and cultural heritage of the area, including the conservation of biodiversity and improvement of local facilities (Fillion *et al*., 1994).

Ecotourism is increasingly seen as a means to promote wildlife conservation, increase public awareness, and raise revenue for protecting endangered species. Unfortunately, rapid, unmonitored development of ecotourism projects can lead to degradation of habitats and deleterious effects on animal well-being. Habituation of animals to human presence can increase the likelihood that animals will actively seek out contact with humans, particularly in the form of crop raiding and invasion of garbage pits, latrines, and human households. Habituation may lead to alterations in animal stress responses, and this may lead to immunosuppression, increasing susceptibility to infectious diseases, and decreasing reproductive success.

Other risks may include pollution, crowding, introduction of invasive species, and transmission of pathogens through direct and indirect infection routes. Zoonotic (nonhuman animal to human) and anthropozoonotic (human to nonhuman animal) infection transmission are of vital consideration, given the increasing demand from tourists to experience direct encounters with wildlife. It is therefore important to produce definitive guidelines that will protect visitors from possible risks as well as ensure long-term well-being of the animals. To outline proper development and implementation of ecotourism activities, many documents stress that travelers should be educated about the importance of conservation, and that tour operators should instruct travelers to minimize impacts while visiting sensitive environments (Ceballos Lascur'ain, 1996; WTO, 1999; Epler Wood, 2002; WTO, 2002; Eagles *et al*., 2002; Christ *et al*., 2003; Higginbottom, 2004; WTO, 2005).

However, human or nonhuman animal health is not usually discussed, except in reference to the need for healthy employees. For example, the American Society of Travel Agents' Ten Commandments on Ecotourism recommends not disturbing animals or purchasing products made from endangered species, but there is no mention of zoonotic/anthropozoonotic diseases. Health information is not currently available on commercial travel Web sites (Horvath *et al*., 2003). The International Society of Travel Medicine's Responsible Traveler handout does not discuss zoonotic/anthropozoonotic infections. It is long overdue that a line of communication be opened among conservation biologists, ecotourism practitioners, and travel medicine specialists, particularly in regards to primate-based tourism.

Primate-Based Ecotourism

Great ape ecotourism began with orangutans in the early 1960s, focusing primarily on ex-orphans during their rehabilitation process to the wild in Sepilok (Sabah, Malaysia), then later in Semanggoh (Sarawak), Tanjung Putting (Kalimantan), and Bohorok (Sumatra) (Rijksen & Meijaard, 1999). Gorilla tourism was initiated in the early 1970s in countries such as Democratic Republic of Congo, Rwanda, and later Uganda (McNeilage, 1996; Butynski & Kalina, 1998). Unlike orangutan tourism, these activities were focused on wild groups. Over the past decade, new ecotourism projects focusing on chimpanzees and lowland gorillas have been initiated in most great ape African range countries. Today, more than 15 sites have developed wild great ape viewing in Central and East Africa, adding to the possible risks of pathogen transmission between wild populations and tourists. Infection transmission between humans and nonhuman animals has typically focused on zoonoses, and rightfully so. Over half of all human infections are zoonotic in origin (Woolhouse & Gaunt, 2007) and several pathogens have been transmitted from nonhuman primates to humans, including simian/human immunodeficiency viruses, simian foamy virus, simian T-lymphotropic virus, *Plasmodium knowlesi*, and *Cryptosporidium* (Gao *et al*., 1999; Nizeyi *et al*., 2002; Wolfe *et al*., 2004; Singh *et al*., 2004; Jones-Engel *et al*., 2005; Wolfe *et al*., 2005). Wild primates also function as reservoirs for a number of human infections, including filariasis, yellow fever, and Chikungunya virus (McIntosh, 1970; Mak *et al*., 1982; Monath, 2001).

Because of their genetic relatedness with humans, nonhuman primates are particularly susceptible to human infections. They are usually immunologically naıve to these pathogens, and primate populations can be quickly decimated because of the slow reproductive rates of most species, particularly great apes. Various infection transmission events from human to nonhuman primate populations have been suspected (Rolland *et al*., 1985; Goodall, 1986;

MacFie, 1996; Wallis & Lee, 1999; Nizeyi *et al*., 2001; Graczyk *et al*., 2002a), but only a few have been definitively confirmed: human respiratory syncytial virus and metapneumovirus in chimpanzees in Cote d'Ivoire (Kondgen *et al*., 2008) and intestinal pathogens *Giardia* and *Escherichia coli* in mountain gorillas and chimpanzees in western Uganda (Graczyk *et al*., 2002b; Goldberg *et al*., 2007; Rwego *et al*., 2008). Polio and measles, both vaccine-preventable diseases, have caused very high mortality in chimpanzee and gorilla populations (Kortland, 1996; Byers & Hastings, 1991). Primates are also particularly susceptible to tuberculosis of human and cattle origins (Brack, 1987). This is problematic because tuberculosis is easily spread and can survive in the environment for long periods of time. It is critical to note that all the documented and suspected transmission events from humans to wild nonhuman primates involved local human populations (local residents, researchers, and park personnel), *not* tourists. To our knowledge, no previous study has attempted to adequately document infection transmission from tourists using biological samples. Despite this fact, the risk of anthropozoonotic infection transmission from tourists is likely significant, and may result from both direct contact between tourists and wildlife and aerosolization of pathogens. At Asia's most frequented wildlife tourism destination, the Sepilok Orangutan Rehabilitation Centre in Sabah, a significant proportion of visitors are not adequately vaccinated, and many underestimate their own risk of infection as well as their potential contribution to pathogen transmission (Muehlenbein *et al*., 2008). Despite their interests in environmental protection and known travel to view endangered animals, tourists very likely create unnecessary risk of infection transmission to wildlife because they are largely unaware of the impacts they may directly have on animal health.

Current and Future Protective Guidelines at Great Ape Tourism Locations

Most great ape tourism projects follow similar rules that intend to minimize possible animal disturbances, negative impacts on the habitat, and risks of infection transmission. Participant minimum age ranges from 12 to 15 years, animal viewing distance ranges from 7 to 10 meters, visit duration ranges from 1 to 2 hours, and tourist group size ranges from five to eight persons. For all sites, any animal group can only be visited once per day. Orangutan visitation in Sabah (Red Ape Encounters) further limits tourist visitations to 15 times per month for each animal. For all sites, visitors are required to voluntarily report any illnesses, from cold sores to influenza to diarrhea, and registration and briefings are required before animal viewing. Groups of tourists should remain together and use appropriate body language, observing the animals quietly. Human feces must be adequately buried, and littering, smoking, eating, flash photography, feeding or touching animals, coughing, spitting, or nose blowing are not permitted. Project personnel may also be subject to varying requirements, such as current vaccinations, negative tuberculosis tests, annual health inspections, and disinfection of clothing and footwear (MGVP, 2004). Several additional recommendations have been made (Wallis and Lee, 1999; Homsy, 1999; Woodford *et al*., 2002; Leendertz *et al*., 2006; Goldberg *et al*., 2007; Rwego *et al*., 2008; Muelhenbein *et al*., 2008) including the use of disposable facemasks, hand washing with soap and clean water, and shoe disinfection with a mild bleach solution before and after visitation with the animals, proof of current vaccinations, use of improved tourist brochures, educational seminars or instructional videos with rules and justifications, detailed protocols for outbreak identification and reporting, and punishment for those tourists and guides who disregard the rules. The risks of pathogen transmission likely vary by location and primate species in question (ie macaques vs gorillas, forest vs savanna habitat, wild vs rehabilitated animals, etc.), and thus several of the prevention measures may vary by location/species, whereas other prevention measures warrant standardization. Adoption of some of these practices may result in lower immediate revenue, but at the benefit of ensuring long-term utilization of these animals. Implementation of these prevention measures will certainly require additional funding for new infrastructure, supplies, and personnel. Tightening some of the rules may even widen the gap between tourist demand and available opportunities.

It is the combined responsibility of the tourism and medical communities to accurately communicate the risks of zoonotic and anthropozoonotic infections in ways that best support the needs of humans and wildlife alike. Such educational initiatives would be facilitated if accurate data existed on any actual links between disease and wildlife tourism. In the interim, there is little doubt that we must be conscious of the impacts that human–wildlife interactions may have on disease ecologies, and efforts would be supported if more resources were devoted to initiatives in conservation medicine with collaborations among physicians, veterinarians, epidemiologists, and conservation biologists. Such collaborations will facilitate much-needed reconciliation on the potential impact that anthropozoonotic infections from tourists can have on wildlife populations.

Feedback Sought from Travel Medicine Specialists

The Species Survival Commission, International Union for Conservation of Nature, Section of Great Apes is currently formulating best practice guidelines for wild great ape tourism. Past efforts to formulate proper tourism guidelines at primate locations have, for whatever reasons, been dominated by conservation biologists and infectious disease specialists, often involving many who do not specialize in ape disease ecology or human health behaviors, with a general lack of past interaction between travel health and anthropology. The primary purpose of the present communication is to facilitate the development of relationships among conservation biologists, ecotourism practitioners, and travel medicine specialists, particularly in reference to primate-based tourism. Perhaps, these needs would be best met via the formation of a task force or interest group of travel medicine specialists to begin to address some of the following:

- What are the benefits and feasibility of requiring vaccination certificates of visitors at primate-tourism locations? How could such a program be implemented?
- Should the minimum age limit of visitors be increased, possibly to 18 years of age, to avoid the introduction of some childhood diseases?
- Is there utility in implementing a ‘‘quarantine,’’ so that visitors should be in-country for a number of days before visiting the wildlife sanctuaries?
- What are the best ways to get ecotourists to voluntarily participate in illness screenings and honestly self-report illnesses when they know that ill people will be denied entrance to the park? Is there benefit in screening participants for illnesses? Who is qualified to enforce this?
- How useful would requiring disposable facemasks be? They may be less effective in humid weather and will likely impede tourist experiences.
- What may be the best strategies to increase participant compliance in hand washing and shoe disinfection?
- How can tourists become informed about animal health before they leave their countries of origin?
- What is the feasibility of making any of these recommendations part of the World Health Assembly’s International Health Regulations?

We encourage those interested in the subject to contact us, or to initiate a discussion in the correspondence section of the *Journal of Travel Medicine*. The global management of zoonotic and anthropozoonotic epidemics is an obligation that transcends any one discipline. Discussion of these problems would complement real-time health monitoring of human–wildlife interactions, which will ultimately function to ensure the sustainability and growth of ecotourism. Understanding the risks of pathogen transmission from humans to wildlife is a necessary but often overlooked aspect of wildlife conservation. In this case, any benefits we make to wildlife health will ultimately benefit human health.

CHAPTER 6

GENERAL DISCUSSION

1. Orang-utan status in Sabah

One of the key elements that significantly improved the orang-utan conservation status in the state of Sabah over the past fifteen years has been the acquisition of precise knowledge about the population size, the distribution, and the status of the species. In the early 2000s no precise published data about orang-utan population size and exact distribution was available for the State, except for Payne (1988). It was generally assumed that the network of protected areas that was already established would ensure the viability of the species in the long-term. At that time, the network of protected forests comprised 153 patches, representing 1,150,598 ha or slightly more than 14% of the total landmass of the state (Table 6.1). Commercial forest reserves (or forests exploited for timber) accounted for 2,665,900 ha.

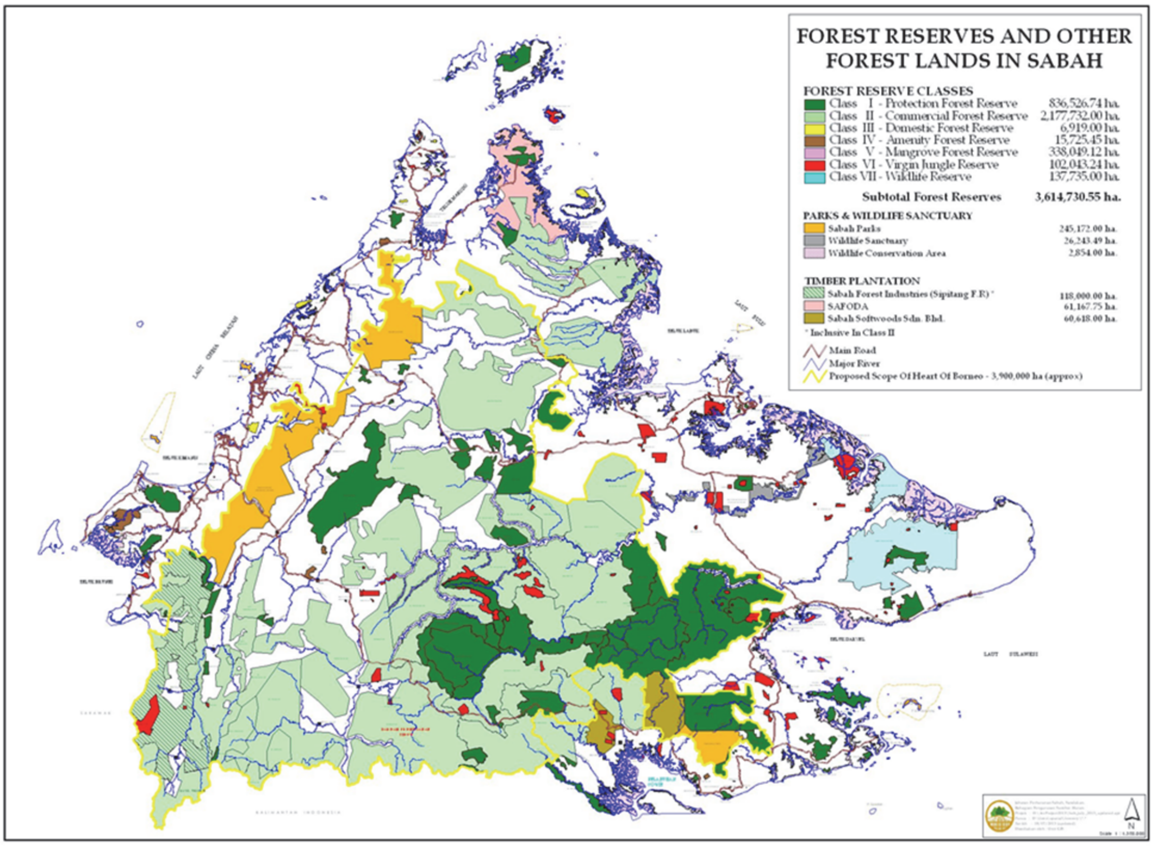
By combining aerial and ground surveys, the 2002 state-wide orang-utan survey showed that Sabah was home to approximately 11,000 orang-utans (Ancrenaz *et al.*, 2005), a number significantly higher than would have been expected from the scientific knowledge available previously (Payne, 1988; Rijksen & Meijaard, 1999). This survey also established that most orang-utan populations in Sabah were located in unprotected multiple-use forests exploited by private companies and local communities for timber, agriculture and other uses. Finally, these surveys also confirmed that the vast majority of protected forests occupied by orang-utans in Sabah had been exploited in the past before being afforded a protection status. Therefore they were not free of human influence and some of them were severely logged-over and degraded. The maps and figures produced by the 2002 Sabah state-wide aerial surveys gave a powerful image of orang-utan distribution and status: they identified the location and size of key populations throughout the state (Ancrenaz *et al.*, 2005). This information was used by the local government and key stakeholders to make crucial decisions for orang-utan conservation in Sabah, culminating in the development of an “Orang-utan Action Plan” for the state of Sabah, which was launched in 2012 (SWD, 2012).

*Table 6.1: Status of protected areas and commercial forests in Sabah compared to orang-utan population size and orang-utan habitat size in 2005 (source: Sabah Forestry Department website www. http://forest.sabah.gov.my/en/; Ancrenaz et al., 2005). SFD: Sabah Forestry Department; SWD: Sabah Wildlife Department. Note: Class 1: Protection Forest Reserve -FR- (maintenance of forest essential on climatic or physical grounds); Class 2: Commercial FR (production of timber); Class 3: Domestic FR; Class 4: Mangrove FR; Class 5: Community FR; Class 6: Virgin Jungle FR (research purpose); Class 7: Wildlife FR; * The Lower Kinabatangan Wildlife Sanctuary was officially gazetted as a protected area in 2005 only.*

Status	Agency	Number	Size (ha)	Orang-utan habitat size	Orang-utan population
National Parks	Sabah Parks	3	243,216	90,000	250
Protected forests class 1-4-5-6-7	SFD	149	881,279	305,000	2,800
Wildlife Sanctuary*	SWD	1	26,103	21,000	1,100
Total Protected Areas		**153**	**1,150,598**	**416,000**	**4,150**
Commercial forests (class 2-3)	SFD	32	2,665,900	1,243,000	6,800
TOTAL		**185**	**3,790,395**	**1,653,000**	**10,950**

The immediate priority recognized for orang-utan conservation in the state was to ensure a higher protection status for some of the key populations identified in Sabah. First, the State Cabinet finally endorsed the “Lower Kinabatangan Wildlife Sanctuary” in 2005, which added 26,000 ha of extreme lowland forests (*i.e*. below 50 m asl) to the growing network of protected areas. In the early 2000s the Lower Kinabatangan was home to about 1,100 orang-utans (Ancrenaz *et al*., 2004b). Although the number of animals is still declining today in the area (KOCP, *unpublished data*), the population in Kinabatangan remains one of the key orang-utan populations for Sabah and for Malaysia (SWD, 2012).

The 2002 surveys also established that the largest unfragmented orang-utan population in Malaysia (about 4,500 wild orang-utans) occurred in the unprotected commercial forest reserves of the Ulu Segama-Malua-Kuamut-Kalabakan complex (Ancrenaz *et al*., 2005; Chapter 2). These forest reserves have been logged several times since the 1960s. At the end of 2007, following the last logging cycle, the government banned logging activities in Malua and in Segama for a ten year period (Chapter 2). In 2012, full protection status was given to these forests, adding 182,000 ha of fully protected forests, most of them being extreme lowland areas (i.e. below 50 m asl). In 2013, the State government regazetted an additional 240,000 ha of commercial forest reserves (Class 2) into strictly protected forests (Class 1) after a last round of logging. This decision was mostly based on the presence of orang-utans in these forests (parts of Gunung Rara, Kuamut and Kalabakan Forest Reserves). Today, the current network of terrestrial protected areas in Sabah covers approximately 18% of the state (Fig. 6.1). More importantly for orang-utan conservation, this network harbors about 70% of the total number of animals living in the state as opposed to about 40% in the early 2000s (Ancrenaz *et al*., 2005).



Map 6.1: Map showing the location and extent of fully protected forests in the state of Sabah as of early 2014: dark green, orange and grey areas are fully protected areas (source: Sabah Forestry Department [SFD], 2014).

2. The value of protected areas to conserve orang-utans

Undoubtedly, establishing protected areas is an effective tool and is needed to conserve biodiversity (Laurance *et al*., 2012a). However, the ability of protected areas to preserve biodiversity in the long-term is challenged by many factors, in Sabah and elsewhere:

(1) Many taxa and ecosystems are poorly represented in the network of protected areas. For example, in Borneo, most protected areas occur in highland areas with

steep slopes, or in remote places considered to be unsuitable for agriculture. Establishing more protected areas in lowland areas would be a much more effective tool to mitigate the current land-use transformations that threaten orang-utans in Borneo, and other species worldwide (Hoffman *et al*., 2010);

(2) The network of protected areas is too fragmented to provide sufficient space of appropriate habitat for wide-ranging populations, such as large mammals and migratory birds (Bruner *et al*., 2001);

(3) It is uncertain whether the network of protected areas will be able to maintain biodiversity in a changing environment impacted by dynamic processes such as global climate change (Bruner *et al.*, 2001; Rodriguez *et al*., 2004; Gregory *et al*., 2012);

(4) Worldwide, many protected areas are in crisis: they are threatened by direct encroachment and illegal activities, lack the necessary support of local communities, are poorly managed and suffer from underfunding (Wilson, 2003; Borrini-Feyerabend *et al*., 2004);

(5) The integrity of protected areas depends on complex ecological processes that extend well beyond their legal/geographical boundaries. Therefore, their functionality not only depends on changes within their boundaries (hunting, logging and other encroachment) but just as importantly on changes which occur outside (De Fries *et al*., 2010).

Unlike in Sabah, in Indonesian Borneo (Kalimantan) more than 60% of orang-utan range is located outside the network of protected areas (Wich *et al*., 2012a). Although protected forests should remain one of the cornerstones for orang-utan conservation in Borneo, it is highly unlikely that all forests containing orang-utans are going to be protected in the future. The long-term survival of the species in Borneo will therefore heavily rely on the ecological conditions, health and functionality of unprotected forests, on improved management of unprotected landscapes, and on minimizing losses among orang-utan populations living in unprotected areas. This requires a major change in strategy as to how orang-utan conservation should be practiced (Meijaard *et al*., 2011c).

3. Value of commercial forests exploited for timber for orang-utan conservation

It is now well established that conventional logging has a significant negative impact on biodiversity because of the structural and incidental damage to the forest resulting from timber extraction. A recent meta-analysis showed that primary forests are irreplaceable in terms of retaining certain species restricted to tropical forests. It also showed that in general selectively logged forests can maintain a relatively high level of biodiversity in the tropics (Meijaard *et al*., 2005; Gibson *et al*., 2011), and in Borneo in particular (Meijaard and Sheil, 2007; Berry *et al*., 2010; Rustam *et al*., 2012). Although there is a concern for "overselling" the positive value of exploited forest for biodiversity conservation (Didham *et al*., 2011; Laurance *et al*., 2012a), most conservation scientists are now convinced that exploited forests are worth protecting for the ecological value they still retain (Meijaard *et al*., 2005; Lugo, 2009; Sodhi *et al*., 2010; Edwards *et al*., 2010).

The recognition that selectively logged forests can maintain orang-utan populations is now gaining momentum (Husson *et al*., 2009; Chapter 2), although it was fiercely debated for a long time (Rijksen & Meijaard, 1999; Delgado & van Schaik, 2000; Knop *et al*., 2004). Deramakot Commercial Forest Reserve illustrates that sustainable logging practices can be reconciled with orang-utan conservation. Deramakot covers 55,000 ha in the upper Kinabatangan area. In 1997, Deramakot was the first natural forest exploited for timber to be certified as "well managed" by the "Forest Stewardship Council" (FSC) in South East Asia (Lagan *et al*., 2007). Under FSC guidelines, selective and reduced-impact logging practices are designed to balance environment, the needs of local communities and considerations of financial returns. Sustainable practices must follow certain rules to limit the damage to trees and to the forest: preparation and implementation of a detailed pre-harvesting conservation plan that precisely identifies the trees to be harvested, identification and protection of crucial ecological resources from damages and human disturbances (riparian habitat, patches of rich forest, major food sources, etc.), design of a low impact road system, implementation of reduced-impact logging practices such as directional felling and a strict policy of prohibiting the hunting and killing of wildlife. If well implemented, these practices have a relatively low impact on forest structure and composition (Putz *et al*., 2012). Typically, only a few trees are removed per ha, mostly members of the Dipterocarpaceae family. The gaps created in the canopy by the removal of a few emergent trees favor light penetration and are colonized by pioneer and light-demanding plant species. These pioneer trees and climber plants produce fruits and young leaves more often and more regularly than climax tree species, offering alternative food sources to fruit-eater species during periods of low fruit productivity (Marshall *et al*., 2009b).

The wildlife monitoring designed in 1999 for Deramakot aimed to assess the impact of forest management practices on the well-being of wildlife populations and included regular ground and aerial orang-utan nest counts (Ancrenaz & Lackman, 2000). The results of the aerial nest counts showed that the orang-utan population has been stable in Deramakot over the past 15 years, with densities fluctuating between 0.8 and 2.2 individuals/km^2 (SFD, 2012). Although it is still too early to generalize the results of the Deramakot model to other forests exploited for timber, regular orang-utan monitoring conducted by the Sabah Forestry Department, KOCP and other partners in commercial forest reserves throughout Sabah confirm that the species can be found in logged forests in the absence of hunting, and is therefore more resilient to forest exploitation than previously assumed by the scientific community (Chapter 2).

These new findings establish that better forestry practices could significantly improve orang-utan and biodiversity conservation in commercial forests. Sustainable logging may be compatible with orang-utan survival as long as it involves diligent planning, proper implementation of reduced-impact practices, and strict enforcement of a zero-hunting policy of wildlife. Considering that forests exploited for timber represent the major part of the range of great apes in Asia and also in Africa, the implementation of sustainable timber harvesting practices in these forests is the key to maintain most populations in the long-term (Wich *et al*., 2012a; Morgan *et al*., 2013; Chapter 2).

In Sabah, FSC certification is seen as a guarantor for the long-term supply of timber. The state government has decided to certify all remaining exploited natural and planted forests by the end of 2014 (SFD, 2012). However, the costs of certification remain an obstacle for most timber companies in South East Asia, and stronger economic incentives need to be implemented in order to promote sustainable forestry practices at a larger scale (Dennis *et al*., 2008).

4. Potential value of agricultural landscapes to sustain wild orang-utans

The latest knowledge on orang-utans shows that approximately half of their current range in Borneo falls within forest areas earmarked to be converted to agriculture or other types of land-use such as mining or industrial tree plantations (Wich *et al*., 2012a). Thus, the future of the Borneo orang-utan depends on the economic and political choices that are currently made by the governments of Indonesia and Malaysia. This situation also indicates that adequate conservation planning for the species cannot restrict itself to the network of fragmented protected and unprotected forests but also needs to consider the highly modified human-transformed landscapes adjacent to natural forests (Wilson, 2007; DeFries *et al*., 2010; Foster *et al*., 2011; Wich *et al*., 2012a).

If the transformation of forests into non-forest landscapes is done without adequate large-scale land-use planning and its appropriate implementation, forest conversion has a devastating impact on its original biodiversity in general and resident orang-utan populations in particular. When forests are replaced with crops, most animals disappear (Meijaard *et al*., 2011a). In the Kinabatangan for example, a recent genetic analysis showed that the surviving orang-utan population represented a mere 5% of the original population. This drastic decline was associated with the onset of mechanical forest exploitation and forest conversion to agriculture, mostly oil palm industry (Goossens *et al*., 2006b).

In these newly created man-made landscapes, the ultimate and long-term impact of human disturbance on biodiversity is strongly influenced by the general configuration of the landscape after habitat loss and alteration (Forman 2006; Hilty *et al*., 2006; Lindenmayer & Fisher, 2006). It is therefore imperative to investigate what is the potential (if any) of the industrial-scale agricultural landscape for orang-utan and biodiversity conservation. At the same time, it is also important to ensure that agricultural landscapes will retain some functional ecological role to guarantee a minimum level of ecosystem services (Foster *et al*., 2011).

Scientists have neglected until very recently to study the use of agro-industrial tree plantation by orang-utans. Recent studies report orang-utan presence in a mosaic of mixed agriculture and forests (Campbell-Smith *et al*. 2011a; Campbell-Smith *et al*., 2011b), in mature agro-industrial plantations of oil palm (Chapter 3), or in acacia plantations (Meijaard *et al*., 2010). Orang-utan presence in these highly transformed habitats brings hope in the struggle to balance development and species survival. Because current information suggests that these agro-industrial plantations cannot sustain viable orang-utan populations in the long-term (Meijaard *et al*., 2010; Chapter 3), these landscapes could at least provide essential connectivity between areas of natural forest (Wich *et al.*, 2012a). Better management practices for agro-industrial plantations could minimize the strong negative impacts of agro-industrial development on overall orang-utan population viability. From the data collected in Sabah (Chapter 3), it is clear that the conservation paradigm for orang-utan within the agro-industrial landscape must include the preservation and/or restoration of small patches of forest. Used as corridors or stepping-stones, these forest patches (even if degraded) play an important role in sustaining orang-utan populations by providing dispersal or food resources. All remaining forests and forest patches located within an industrial landscape should be identified as “High Conservation Value Forests” and should be maintained as forests. Indeed, retaining forests within an agro-industrial landscape is the key to maintain ecosystem functionality, because it ensures the viability of meta-populations of many wildlife species through facilitating dispersal and survival (Maddox *et al*., 2007; Mc Shea *et al*., 2009).

Many relevant recommendations have already been included in broader guidelines for several certification schemes such as sustainable oil palm (the Round Table for Sustainable Palm Oil – RSPO), sustainable timber extraction (Forest Stewardship Council - FSC), and others. However, it is currently not clear whether certification schemes will really mitigate environmental and biodiversity impacts of agro-businesses as they are supposed to, for several reasons: difficulty to make principle and criteria operational, reluctance by the industry to compromise on yield and profit, difficulty in documenting the actual biodiversity and ecological processes we want to maintain, and reluctance of consumers to pay for a premium which certification might entail (Laurance *et al*., 2010; Paoli *et al*., 2010; Traeholt & Schriver, 2011; Koh & Lee, 2012; Meijaard & Sheil, 2012). We have to accept that certification is not the only solution. It is part of an arsenal of tactics that must be developed to fulfill the global needs and desires of humankind while safeguarding the environment as much as possible (Nesadurai, 2013). Additional methodologies need to be also promoted: raising yield efficiency through better technology, increasing production and transportation efficiency, transitioning to diets that are less protein-rich, reducing individual consumption rates and diversifying the primary production of the landscape (Koh, 2011; Sunderland, 2011; Koh & Lee, 2012).

5. Orang-utan: a highly adaptable and versatile species?

Historically, the orang-utan has been often described as extremely sensitive to forest degradation and it was believed that large intact patches of primary forests were necessary to sustain viable populations in the long-term (Riksen & Meijaard, 1999; Delgado & van Schaik, 2000). Because of this view, setting aside protected forests became the cornerstone for orang-utan conservation. Recent studies conducted in Kinabatangan and in other degraded parts of Borneo showed that the species was more adaptable and versatile than originally thought. Inter-population differences were highlighted in a recent cross-site comparison conducted throughout Borneo and Sumatra (Wich *et al*., 2009). Across sites, scientists have identified more than 1,500 species of plants as being part of the orang-utan diet, which is markedly higher than the number of species consumed by African apes – a few hundreds for each species - (Russon *et al*., 2009). It is now well established that food availability, accessibility and nutritional value are some of the major determinants of overall fitness, dominance status, reproductive and social successes of primates in general (Altmann, 1998; Altmann & Alberts, 2005; Emery Thompson, 2013). However, we know relatively little on how food selection and food choice can impact reproductive and survival rates of individual orang-utans and overall populations (Knott *et al*., 2009). In addition, the underlying factors responsible for differential food preferences observed among different orang-utan populations are still unclear (van Schaik *et al*., 2009). Although orang-utans can use a high number of plants and therefore could potentially shift their diet during periods of food scarcity or when original resources are altered following intense degradation, we still need to understand how feeding on sub-optimal food sources for extended periods of time will impact the overall fitness of individuals and their reproductive success.

Other characteristics such as start and duration of daily active period, time budgets or daily distance traveled fluctuate between populations in accordance with variation in forest types and stage of forest degradation or regeneration (Morrogh-Bernard *et al*., 2009), reinforcing the idea that different populations will match their ecological requirements to available resources. In fact, different populations will show differing ecological phenotypes, ranging from a “sit and wait” strategy in places where food availability is highly seasonal to a “search and find” strategy in places where food availability is more regular (Morrogh-Bernard *et al*., 2009). Differences between populations are further indicated by the variety of cultures and cognition skills recorded throughout the range of both species in Borneo and Sumatra (van Schaik *et al*., 2009).

Although orang-utan has been studied for several decades, its ecology is still far from being completely documented and understood. Today, new discoveries are still being made about the species, leading to a better understanding of its ecological needs. A good example is the recent cross-site analysis of camera-trap photographs which showed that the species was walking on the ground more regularly than previously thought (Chapter 4). This analysis reveals that terrestrial locomotion of Bornean orang-utans is quite common in all age-sex classes and not restricted to the larger and heavier flanged males as often described (Rijksen & Meijaard, 1999). Our analysis also showed that the degree of orang-utan terrestriality is influenced by forest type and structure, suggesting in turn that forest disturbance (natural or man-made) and creation of larger gaps in the canopy will result in increased terrestrial activity. This terrestrial behavior is not as surprising as it may appear at first glance since the potential ancestors of *Pongo* are thought to have used more ground locomotion than modern orang-utans (Harrisson and Chivers, 2006; Begun & Kivell, 2011) and were therefore able to cover larger distances on the ground (von Koenigswald, 1982; Wich *et al*., 2009). The capacity of orang-utans to cross open spaces on the ground may increase their ability to cope with at least smaller scale fragmentation and to roam in mosaic landscapes, although the extent of this adaptability remains to be investigated (Chapters 3 and 4).

All these findings illustrate the potential of the orang-utan to adjust to changes in ecological conditions due to natural or to anthropogenic causes. This versatility can explain that the species can sometimes be found in highly transformed landscapes, and this needs to be incorporated in new orang-utan conservation strategies (Meijaard *et al*., 2011b; Wich et al., 2012a). However, orang-utan presence in man-made landscapes exposes them to a whole series of new risks: closer proximity to people; increased likelihood of crop-raiding activities; increased susceptibility to become a target for hunting; and increased exposure to new diseases.

6. New habitats, new sanitary risks

Diseases can play a significant role in the decline and extinction of wildlife species; they are currently recognized as one of the major threats for wildlife persistence (Leendertz *et al*., 2006). The occurrence of emerging infectious diseases is also a major threat to global public health, with high economic impacts. They result from complex demographic and anthropogenic environmental changes including global climate change, urbanization, increased penetration of natural ecosystems by people, international travel and trade, land use change and agricultural intensification, and the breakdown of public health (Daszak *et al*., 2013).

In general, great apes are susceptible to many pathogens from human origin: human respiratory syncytial virus (Kongden *et al*., 2008); polio and measles (Kortlandt, 1996; Byers and Hastings, 1991); intestinal pathogens (Grazcyk *et al*., 2002; Goldberg *et al*., 2007; Rwego *et al*., 2008); tuberculosis, transmitted by both people and cattle, anthrax (Leendertz *et al*., 2004) and many other pathogens (Wallis & Lee, 1999; Nizeyi *et al*., 2001). There is still very little knowledge on the pathogens present and the diseases of wild orang-utans in Borneo and Sumatra. Therefore, the epidemiology and dynamics of emerging diseases that could potentially affect great ape populations in human-made landscapes need to be investigated thoroughly. Although more and more resources are dedicated to study disease ecology and conservation medicine, an understanding of these processes requires interdisciplinary efforts and significant time and financial resources. Responsible health monitoring of interactions between people and wildlife, especially when the species come in close contact as at ecotourism destinations, becomes more urgent (Chapter 5). Only then, will we be in a position to prevent entirely avoidable great ape population declines that come from a lack of sanitary precautions (Kongden *et al*., 2008).

One of such studies was recently conducted at the KOCP intensive study area. “Red Ape Encounters (RAE)” is a community-based eco-tourism initiative that was established in the Lower Kinabatangan in 2001 with the aim to trek with wild habituated orang-utans in the Kinabatagan (Ancrenaz *et al*., 2007). In order to minimize “stress”, reduce the risks of disease transmission to the visited animals and reduce negative impacts on the fragile forest ecosystem, strict visitor guidelines were developed, implemented and monitored (Rajaratnam *et al*., 2007). These guidelines are currently endorsed as best management practices for great ape ecotourism (MacFie & Williamson, 2010). In order to test the efficiency of these guidelines, we conducted a fecal cortisol analysis of wild habituated and non-habituated orang-utans in conjunction with tourism activities (Muehlenbein *et al*., 2012). The results of this study showed that tourist visitation was correlated with higher cortisol levels in wild habituated orang-utans used for tourism activities, and that the fecal glucocorticoid metabolite levels of habituated individuals were lower than for non-habituated animals. In other words, these results showed that wild habituated orang-utans used for tourism activities were not chronically stressed, as long as the tourism guidelines developed and implemented by RAE were enforced. The experience in the Kinabatangan shows that responsible tourism practices can produce quality-viewing opportunities while continuing orang-utan conservation. However, the difficulties involved in developing and implementing high quality great ape based tourism products need to be recognized (Rajaratnam *et al*., 2007; MacFie & Williamson, 2010): ecotourism is not a panacea, but merely one of the tools available for great ape conservation.

7. Possible role of local communities for orang-utan conservation.

Subsistence of viable populations of orang-utans and other wildlife in heavily transformed landscapes will ultimately depend on the general perception of human communities who share the same environment. People's perception and acceptance of wildlife is a complex combination of factors related to economy (is wildlife perceived as a source of loss because of conflicts or a source of gain through ecotourism and other services?) or valued for other purposes such as an individual appreciation of animal's proximity for recreation, the place of animals in traditional culture and folklore, and awareness (Meijaard *et al*., 2013).

Wildlife presence in newly created human-made landscapes such as agricultural lands often results in the increase of crop-raiding activities and conflicts. These conflicts lead to emotional distress and occasionally to significant economic losses (Nepal & Weber, 1995; Chung *et al*. 2007; Campbell-Smith *et al*., 2012). Worst, the occurrence of conflicts creates a negative perception towards wildlife (Campbell-Smith *et al*., 2012) and becomes a major impediment to building local support for conservation (Webber *et al*., 2007; Marchal & Hill, 2009; Gore & Kahler, 2012; Meijaard *et al*., 2014). Successfully addressing conflicts between wildlife and humans requires the design and implementation of technical solutions that decrease or suppress the damages (Hockings & Humle, 2009). But for a strategy to yield long-term success, it also needs to integrate the underlying societal and stakeholder dimension to the problem (Dickman, 2010).

Orang-utans kill acacia trees by stripping bark and cambium (Meijaard *et al*., 2010); they pull out stems and destroy young palms to feed on the heart of the plant (Yuwono *et al*., 2007; Chapter 3). They can also consume entire fruit crops in orchards belonging to local villagers (Campbell Smith *et al*., 2011b). Recent interview surveys conducted in Kalimantan revealed that in many man-made landscapes, killing the "pest" animals was often seen as the ultimate solution to mitigate conflicts with orang-utans (Davies *et al*., 2014). However, these surveys also showed that the majority of animals were killed for other reasons, including trade for meat, pets or traditional medicine, or due to fear and ignorance. A complex interplay of variables predicted the risks of orang-utan killing at the local level, with religion being the prime indicator - with Christian people being more likely to kill orang-utans (Davies *et al*., 2014). These interview surveys also concluded that between 2,000 and 3,000 orang-utans have been killed every year over the past three to four decades in Kalimantan – the Indonesian part of Borneo island - (Meijaard *et al*., 2011a), which is well above what the species can sustain (Marshall *et al*., 2009). These new insights show that many orang-utan populations will go extinct within a human generation time if killing continues at the current rate (Meijaard *et al*., 2011c). Under the current scenario, only populations that are living in well managed protected areas or that occur in areas where orang-utan killing is rare (such as Kinabatangan in eastern Sabah: Ancrenaz *et al*., 2007) stand a chance of long-term survival.

As the needs and aspirations of local communities are the ultimate drivers of conservation successes or failures outside protected forests, it becomes clear that we need to encourage these groups to become actors and not only beneficiaries of what conservation can offer (Steinmetz *et al*., 2006; Meijaard *et al*., 2011d). In the Kinabatangan, fifteen years of community-based conservation activities has shown that strong and genuine engagement between local NGOs, government agencies and local communities that share the same environment with orang-utans is necessary to develop a more peaceful attitude towards wildlife conflicts by villagers (Ancrenaz *et al*., 2007). These positive conservation outcomes could be gained through active involvement of community members in conflict mitigation activities, intense capacity building, awareness campaigns and the development of alternative economic opportunities that involve the orang-utan and its forest habitat as a product, amongst other things, for eco-tourism and research (Ancrenaz *et al*., 2007).

8. The need for a paradigm shift for orang-utan conservation in Borneo

Individual people as well as societies have a tendency to categorize ideas and concepts in simple dichotomies (Moll & Shulkin, 2009). This predisposition results in all-or-nothing judgments and biases the vision of the natural world that we would like to preserve. As a result, society emphasizes the value of pristine habitats for biodiversity conservation and tends to neglect modified habitats (Sheil & Meijaard, 2010). Over the past twenty years, the current status-quo opposing protected and non-protected areas has led to increasingly degraded natural ecosystems inside protected areas and to the proliferation of man-made landscapes outside. The land-sparing strategy ignores valuable biodiversity and ecosystem services outside protected areas. A paradigm shift about our comprehension of orang-utan and biodiversity conservation is sorely needed. A binary view that opposes conservation and development creates a division between local communities and people who are living far away from the environmental world they want to protect. This misunderstanding reinforces the feeling of injustice by many people in the tropics regarding how conservation is judged and implemented by individuals or organizations that are not enduring their own hardship (Meijaard & Sheil, 2008; Meijaard & Sheil, 2011). Years of greenwashing or blackwashing campaigns have failed to identify a solution for orang-utan conservation and attest that conserving this species needs different and new approaches (Koh & Sodhi, 2010). For conservation to be more successful, we need to be aware of different viewpoints and to find ways to incorporate them in new conservation solutions (Johns, 2009; Kenwards *et al*., 2011; Doak *et al*., 2014).

Recent theoretical and technical progress allows scientists to move beyond the traditional binary perception of the landscape (protected areas versus non-protected areas) and to assess potential investment priorities in multiple conservation strategies across a variety of land uses (Forman, 2006; Knight *et al*., 2006; Wilson *et al*., 2007). These new tools should allow scientists to rethink their judgments and roles in conservation. In particular, this means moving away from the original vision of pristine environments and to become serious in studying the numerous new challenges created by modern development in newly human-transformed landscapes. Often, the “real-world” conservation challenges are disconnected from the research topics that are investigated by academics (Laurance *et al*., 2012b). Simultaneously, conservation decisions are based more often than not on personal intuition and guesswork rather than on hard science (Sutherland *et al*., 2004). In order to improve on this situation, conservation scientists need to address questions that have a direct implication for applied conservation.

Scientists alone will not change how the world is evolving or what paths are going to be taken by human development. There is, however, an urgent need for scientific outcomes to reach stakeholder groups which are beyond the usual academic circles to ensure that all societal groups are informed: politicians, local communities, private industry, media, and others. In order to reach a wider audience, pro-active and multi-disciplinary engagement is required (Johns, 2005). Creating smart and new alliances will increase the ability of scientists to influence and to convince contemporary human societies about how we perceive orang-utans and more generally biodiversity conservation (Koh & Sodhi, 2012; Koh, 2011). New communication tools such as social media are an opportunity to reach an ever increasing number of people.

We expect that the future of orang-utans (and of many other species) very much depends on the long-term security of large, strictly protected forests where illegal logging and hunting are efficiently controlled and where orang-utan populations are large enough to cope with potential catastrophic events such as fires and diseases (Meijaard *et al*., 2011). These forests need to contain within them the ecological gradients that make key resources available which sustain orang-utans to adapt to climate change and other gradual changes (Gregory *et al*., 2012). In the larger landscape, scientifically-based, regional land use planning is needed to delineate the zones of interaction around protected forests and their surroundings, encompassing hydrological, ecological and socioeconomic interactions (de Fries *et al*., 2010). Ideally, the core protected areas should remain connected with other forests that could be sustainably used for (commercial) timber extraction. Recent spatial analysis in Sumatra and Borneo showed that the level and extent of encroachment was similar between well-managed privately-owned timber concessions and protected forests (Gaveau *et al*., 2009; Gaveau *et al*., 2013), highlighting the possible value of the industry to maintain orang-utan populations in the long-term. Indeed, some of these companies have already obtained certain attributes that could be useful for biodiversity conservation: well-trained staff, significant financial resources, and clear and strong operation protocols for managing their activities, amongst other things. It is therefore urgent to engage with these stakeholders to improve their practices. In turn, these natural forest covered areas could be buffered by low-intensity plantations such as acacia, pulp and paper and other mosaic industrial tree plantations (McShea *et al*., 2009). This landscape would then be connected to high intensity-use areas such as agro-industrial schemes and areas where infrastructures, roads, small-scale agriculture and most people live (Wich *et al*., 2012a).

The design of such living landscapes must be approached across the whole landscape rather than at the site and species level (Morrison, 2009; Sayer *et al.*, 2013): we need to shift the focus from conserving specific sites and species to respecting landscapes and processes and to envision a larger scale landscape approach. Conserving ecosystem functions and services can only happen if environmental concerns are considered at the beginning of the planning process. The best chance to achieve this will require scientists, NGOs, government agencies and the private sector to genuinely engage and work closely together (Doak *et al*., 2014).

ZUSAMMENFASSUNG

Das Naturschutzmanagement und die Naturschutzmedizin des Orang-Utans (*Pongo pygmaeus morio*) in Sabah, Malaysia

Orang-Utans sind die einzigen Menschenaffen Asiens und leben ausschließlich in den tropischen Regenwäldern von Sumatra und Borneo. Die Populationen von Orang-Utans sind in den vergangenen Jahrzehnten stark zurückgegangen. Der Sumatra Orang-Utan (*Pongo abelii*) wird als stark gefährdet und der Borneo Orang-Utan als gefährdet auf der Roten Liste geführt. Als Hauptursachen für den Rückgang der Orang-Utan Populationen gelten die Jagd und die Verwendung als Nahrungsmittel oder für die traditionelle Medizin, der Handel mit ihnen als Haustiere, die Zerstörung, Degradierung und Fragmentierung der Lebensräume sowie wie Krankheiten und der Globale Wandel. In dieser Doktorarbeit präsentiere ich meine Forschungsergebnisse, die innerhalb der letzten 17 Jahre geholfen haben die Artenschutzbemühungen im Malaysischen Staat Sabah zu fokussieren und den Rückgang der Orang-Utan Populationen zu verringern. Darüber hinaus diskutiere ich die Herausforderungen und Gefahren die durch die vielfältige Nutzung der Landflächen entstanden sind. Im Anschluss erörtere ich wie vorhandene neue Technologien und Entwicklungen genutzt werden können, um das Überleben des Orang-Utans über sein gesamtes Verbreitungsgebietes auch in der Zukunft zu sichern. Meine Doktorarbeit befasst sich mit fünf naturschutzrelevanten Themenkomplexen, die für das Überleben der Orang-Utans wichtig sind. Diese sind:

1. **Die potentielle Rolle von nachhaltigen forstwirtschaftlichen Bewirtschaftungsmethoden auf das Überleben der Orang-Utans in kommerziell genutzten Waldgebieten**

Es steht ausser Zweifel, dass durch die Zerstörung von Wäldern durch konventionelle Forstwirtschaft Orang-Utans lokal aussterben können. In meinen Studien konnte ich jedoch zeigen, dass eine nachhaltige Forstwirtschaft mit dem Überleben von Orang-Utans vereinbar ist, solange der Holzeinschlag gewissenhaft geplant und durchgeführt wird und die illegale Wilderei komplett verhindert wird. Deshalb kann die Implementierung von einem besseren forstwirtschaftlichen Management der kommerziellen Waldgebiete einen Beitrag zur Sicherung des Überlebens der Orang-Utans in einigen Gebieten leisten.

2. **Die Notwendigkeit agrar-industrielle Landschaften mit dem Überleben der Orang-Utans zu vereinbaren.**

Im Osten Sabahs werden Orang-Utans immer häufiger in großflächigen Palmölplantagen gesichtet. Obwohl Palmölplantagen keine überlebensfähigen Populationen von Orang-Utans beheimaten können, rechtfertigen diese Beobachtungen weitere Studien wie Landschaften besser geplant werden können um agrar-wirtschaftliche Interessen besser mit dem Überleben der Orang-Utans zu vereinbaren.

3. Neue Entdeckungen zeigen, dass Orang-Utans sich mehr auf dem Boden fortbewegen, als es bisher bekannt war – diese Erkenntnis bedeutet viele Implikationen für die zukünftige Entwicklung von Schutzprogrammen

Aktuelle Technologien wie Fotofallen haben neue Erkenntnisse über das Verhalten und die Ökologie der Orang-Utans geliefert, einer Art über die Wissenschaftler bisher dachten, dass sie sehr gut erforscht wäre. In dieser Studie in der ich einer der Hauptautoren war konnten wir zeigen, dass Orang-Utans sich häufiger auf dem Boden fortbewegen als bisher gedacht. Diese unerwarteten Erkenntnisse eröffnen neue Ansätze für den Schutz der Orang-Utans, insbesondere im Bezug auf das Management und die Naturschutzstrategien von nicht-geschützten teilweise fragmentieren Gebieten.

4. Die Notwendigkeit erhöhte Krankheitsübertragungsrisiken durch Wildtiertourismus und zunehmendem Kontakt mit Menschen in anthropogen-modifizierten Landschaften zu berücksichtigen

Die Möglichkeit über naturnahen Tourismus die lokale Bevölkerung in den Naturschutz einzubinden hat großes Potential sowohl für den Schutz der Wildtiere, als auch für die Sensibilisierung der Öffentlichkeit für den Naturschutz. Außerdem kann dieser Tourismus für die lokalen Bevölkerung eine neue Einkommensquelle bieten. Häufige Besuche der Lebensräume von Orang-Utans bringen Menschen in engen Kontakt mit Orang-Utans und dies kann kontraproduktiv für die Artenschutzziele sein: Verhaltensstörungen, erhöhter Stress und erhöhte Gefahr durch Krankheitsübertragungen können das Ergebnis von schlechtem Tourismuspraktiken sein. Diese negativen Einflüsse müssen angegangen und minimiert werden um langzeitlichen Schutzstrategien für den Orang-Utan zu entwickeln.

5. Die Notwendigkeit viele Entscheidungsträger in den Schutz der Orang-Utans einzubinden

Orang-Utans kommen in vielen unterschiedlich genutzten Waldgebieten vor. Da diese von unterschiedlichsten Entscheidungsträgern gemanagt werden, bedarf es neuartiger inter-disziplinärer Ansätze die über die traditionellen Meinungen über Artenschutzinitiativen wie die Deklarierung neuer Schutzgebiete hinausgehen. Deshalb darf der Schutz der Orang-Utans sich nicht nur um diese Art zentrieren, sondern die Bedürfnisse der Menschen, die den Lebensraum teilen und nutzen, inklusive ihrer finanziellen Interessen müssen berücksichtigen.

Obwohl Schutzgebiete (z.B. Nationalparks oder Wildtierreservate) auch weiterhin das Herzstück beim Schutz des Orang-Utans sein werden, zeigen die Ergebnisse meiner Dissertation, dass zum Schutz der Orang-Utans in Sabah ein Paradigmenwechsel notwendig ist: Der ursprüngliche Ansatz unbewohnte Primärwälder zu schützen ist nicht ausreichend. Der Schutz vom Orang-Utan muss ein verbessertes Management von vielfältig genutzten Lebensräumen beinhalten. Die Aufgabe wird sein die Co-Existenz von Wildtieren und Menschen zu vereinbaren und gleichzeitig die Risiken von Krankheitsübertragungen, die durch die räumliche Nähe entstehen, zu reduzieren.

SUMMARY

Orang-utans, Asia's only great ape, occur solely in the tropical forests of Borneo and Sumatra (great apes include chimpanzees, gorillas, bonobos and orang-utans). Their populations are declining fast: the Sumatran orang-utan (*Pongo abelii*) is critically endangered and the Bornean species (*Pongo pygmaeus*) is considered endangered in the IUCN Red List. The major drivers for the species declines include poaching for meat and traditional medicine; pet trade; destruction, degradation and fragmentation of their habitat; and natural causes such as diseases and global climate change. In this thesis I present results from the research I designed and conducted to guide some of the conservation efforts that have contributed to slowing down the decline of the species in the Malaysian state of Sabah (Borneo) over the past 17 years. I also discuss some of the new challenges and threats faced by the species in the newly created multiple-use landscapes that are currently found throughout most of the species' range. Last but not least, I discuss new technology and opportunities that are currently available to conservationists and that need to be used in order to secure the future of orang-utans throughout its range. My thesis is articulated around five major orang-utan conservation questions that I have been exploring for the past 17 years. These topics are crucial to secure the future of the species. They include:

1. **The possible function of reduced-impact logging and sustainable practices for orang-utan survival in commercial forest reserves**

Without any doubt, destruction of forests following large-scale conventional logging practices can result in the local extinction of orang-utan populations. However the surveys that I led in Sabah have established that sustainable logging can be compatible with orang-utan survival as long as diligent planning, proper implementation of reduced-impact practices and a zero-hunting policy are all strictly enforced. Consequently, implementing better management practices for commercial forest reserves exploited for timber might contribute to securing the future of the species in some areas.

2. **The need to reconcile the agro-industrial landscape with orang-utan survival**

In eastern Sabah, orang-utans are seen more and more frequently roaming into large industrial oil palm plantations. Although oil palm plantations cannot sustain viable populations of orang-utans, these observations warrant further studies to design better landscapes where we can reconcile agriculture practices and orang-utan survival.

3. New evidence showing that orang-utans are more terrestrial than previously thought – an insight with a host of implications for the design of future conservation efforts

The use of new technologies, such as camera-traps, reveal new facts about orang-utan behavior and ecology, one of the species scientists thought they understand well. The study I co-supervised showed that orang-utans move on the ground more often than we thought. These new findings open new thinking for orang-utan conservation that need to be incorporated in management and conservation strategies in non-protected areas.

4. The need to consider risks of disease transmission as a result of wildlife tourism and increased contact with people in human-transformed landscapes

The promotion of nature-based tourism is seen as a way to incorporate local communities in conservation. It has the potential to promote wildlife conservation, increase public awareness and raise local revenue for protecting endangered species such as great apes. However, regular habitat penetration of the orang-utan habitat by people and repeated close proximity between apes and people can also be counterproductive to conservation goals: behavioral disorders, increased stress levels and disease transmission can all result from bad tourism practices. These negative impacts need to be addressed and minimized in order to develop successful conservation strategies in the long-term.

5. The need to engage with a wide variety of stakeholders

Since orang-utans are found in different forests which are exploited by a wide range of stakeholders, their conservation warrants a novel, multi-disciplinary approach which must go beyond the traditional view of conserving species by designating protected areas. Therefore, orang-utan conservation must encompass the needs and aspirations of people who are sharing and exploiting the same habitat, and must include both commercial interests as well as local communities in their management, rather than solely adopting a single-species conservation approach.

The research presented in this thesis shows that although protected areas should remain the heart of orang-utan conservation, the protection of orang-utans in Sabah requires a paradigm shift: the traditional approach of protecting primary pristine habitat empty of people is insufficient. Orang-utan conservation must incorporate improved management of multiple-use habitats where wildlife and people can co-habit, while minimizing the risks of pathogen transmission which might arise from this close cohabitation.

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ACKNOWLEDGEMENTS

This work is the result of 17 years of scientific research conducted by the Kinabatangan Orang-utan Conservation Programme (KOCP) in the State of Sabah, Malaysian Borneo. For permission to work in Sabah, I want to thank the Sabah Wildlife Department, the Economic Planning Unit, the Sabah Biodiversity Council, as well as the Sabah Forestry Department and all government agencies that have supported our work in Sabah.

KOCP would not exist without the extreme commitment of our highly motivated team of about 50 local field researchers who dedicate their life to orang-utan and biodiversity conservation in Sabah. I'm deeply indebted and grateful to them and to their work. During all these years, this team has truly been a source of inspiration to me.

For giving me the opportunity to undertake this doctorate, I sincerely thank Professor Dr Heribert Hofer. Dr Andreas Wilting was instrumental in the completion of this doctorate, without him this undertaking may not have seen its end.

I want to express my gratitude to a very long list of colleagues, peers, friends and people whom I met throughout my years in Borneo, and who contribute directly or indirectly to wildlife conservation efforts in Borneo.

I also want to thank my family, close and distant, for the trust they have given me and for their patience with me when it was needed. For all of you, I dedicate this work.

Working with wild orang-utans in Borneo has been and continues to be a truly remarkable experience. My dreams, my life would be duller without amazing species such as this that share our planet. So last but not least, I thank all the people who are fighting to preserve biodiversity wherever they live. They are an inspiration and bring hope for the future.

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Selbständigkeitserklärung

Hiermit bestätige ich, dass ich die vorliegende Arbeit selbständig angefertigt habe. Ich versichere, dass ich ausschließlich die angegebenen Quellen und Hilfen in Anspruch genommen habe.

Sandakan, den 25.10.2014

Marc Ancrenaz