Conservation Ecology of Bornean Orangutans in the Greater Batang Ai-Lanjak-Entimau Landscape, Sarawak, Malaysia

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in memory of Tok Nan

Abstract

The Bornean Orangutan (*Pongo pygmaeus*) is one of the three great ape species in Asia. *P. pygmaeus* is further divided into three subspecies based on their genetic divergence. These subspecies are also geographically apart from each other; with the Malaysian state of Sarawak having the least number of wild orangutans. In 2016, the threat level for the species was upgraded to 'Critically Endangered' under the IUCN Red List of Threatened Species. The alarming upgrade was due to increased threats to the survival of the species in Borneo, mainly due to habitat degradation and forest loss as well as hunting. The actual orangutan numbers in the wild were still unclear despite the upgrade due to wide variance generated from various statistical methods or survey protocols used to estimate them.

In Sarawak, the conservation efforts have been ongoing with the focus on preventing further population decline, habitat degradation and forest loss. The first step in this effort was to acquire baseline data on population estimates and distribution at the core habitats of Batang Ai-Lanjak-Entimau (BALE) where most of the viable orangutan populations are found in the State. The data were needed for drafting a policy on a long-term strategic action plan for orangutans at the greater BALE Landscape. If the policy is approved, collaboration is anticipated between conservation partners and government agencies to implement the recommendations. These cover a wide range of disciplines including science, technology, policy and socio-economy.

The purpose of this thesis is then to provide a comprehensive and updated report on orangutan conservation in Sarawak for the intended joint collaborators. This thesis expounds on the current threats and conservation strategies in Sarawak, recent population and distribution studies at the Batang Ai-Lanjak-Entimau (BALE) Landscape, and recommendations for future studies at other focal sites with remnant orangutan population outside the core habitats of BALE. One of the major findings include a combined estimate of 355 orangutans with the 95% highest density interval (HDI) of 135 to 602 individuals at the project sites. The outcomes of this project show that the survey designs using Bayesian analyses were a novel approach for site-specific studies, and the results complemented the growing scientific repository on orangutan population studies in Borneo.

I conducted this project in collaboration with the Wildlife Conservation Society (WCS) Malaysia, the organization that sourced the unpublished data used for the analysis of this project. WCS has conducted orangutan nest count surveys at the BALE Landscape since 1991. For the population study, I used new orangutan nest data recorded during the surveys conducted between 2011 and 2015. Subsequently, I combined this data with surveys conducted between 2003 and 2007 as an academic exercise to map proxy orangutan distribution. The survey designs for both the population and distribution studies as shown in the Supplementary Materials were developed by Mike Meredith, the main statistician of this project. I ran the data analysis and compiled the R graphic outputs for the thesis chapters.

This thesis should be of interest to policy makers in the Forest Department, Sarawak Forestry Corporation, private organizations and research institutions, as well as local and international collaborators for the implementation of the policy on zero-loss of orangutans and their habitats. It should also be of interest to scholars of great ape ecology and conservation, as well as of land use planning and protected area management.

Thesis Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

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Joshua Juan Anak George Pandong
19 February 2019

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I dedicate this thesis to the late Tok Nan for his intense efforts to conserve orangutans and to expand protected areas for the critically endangered species in Sarawak.

To Jesus Christ be all glory and honour.

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List of Acronyms

BA	Batang Ai
BALE	Batang Ai-Lanjak-Entimau
BANP	Batang Ai National Park
CI	Confidence Interval
CPO	Crude Palm Oil
CV	Coefficient of Variation
EPI	Environmental Performance Index
ET	Engkari-Telaus
FDS	Forest Department Sarawak
FFB	Fresh Fruit Bunch
FPIC	Free, Prior, Informed Consent
GACF	Great Ape Conservation Fund
GIS	Geographic Information System
HDI	Highest Density Interval
HCVF	High Conservation Value Forests
HoB	Heart of Borneo
IoT	Internet of Things
IUCN	International Union for Conservation of Nature
JAGS	Just Another Gibbs Sampler
LEWS	Lanjak-Entimau Wildlife Sanctuary
MANRED	Ministry of Modernisation of Agriculture, Native Land and Regional Development
MCMC	Markov chain Monte Carlo
MMBF	Margot Marsh Biodiversity Foundation
MNC	Marked Nest Count
MPhil	Master of Philosophy
MYR	Malaysian Ringgit
NCR	Native Customary Rights
NTFP	Non-Timber Forest Products
PABC	Protected Areas and Biodiversity Conservation
PHVA	Population and Habitat Viability Assessment
PPD	Perpendicular Distance
PVA	Population Viability Assessment
SCNC	Standing Crop Nest Count
SD	Standard Deviation
SFC	Sarawak Forestry Corporation
SMART	Spatial Monitoring and Reporting Tools
TPA	Totally Protected Area
UE	Ulu Engkari
UK	Ulu Katibas
UN	Ulu Ngemah
UNIMAS	Universiti Malaysia Sarawak
UP	Ulu Pasin
USD	US Dollar
USFWS	US Fish and Wildlife Service
USM	Ulu Sungai Menyang
WCS	Wildlife Conservation Society
WGS	World Geodetic System
WPO	Wild Life Protection Ordinance
WWF	World Wide Fund For Nature

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Chapter 1.

General Introduction

This MPhil thesis provides a comprehensive and updated report on orangutan conservation ecology in the Malaysian state of Sarawak. Conservation ecology deals with the preservation and management of biodiversity and natural resources; a discipline emerged from the 'accelerating deterioration of natural systems and the worldwide epidemic of species extinctions' [1]. The goal of orangutan conservation ecology then is to find ways to conserve the species, their habitats, landscapes, and ecosystems as efficiently as possible.

This chapter is divided into two sections: 1) the first provides a brief historical context to the Malaysian state of Sarawak in relation to orangutans, and 2) the second outlines the brief structure of subsequent chapters in this MPhil thesis.

Historical background

Sarawak is the single largest state in Malaysia with its land area size of 12.4 million ha, which is almost as large as the whole Peninsular Malaysia at 13.2 million ha [2]. The vastness however is rather deceptive as it consists of approximately 70% hilly inland which are deemed unsuitable for agriculture due to poor soils [3]. Sarawak is characterised by a network of 35 gazetted rivers with a combined length of about 5,000 km [4]. Such varied topography contributes to Sarawak's sparse population. Human settlements are mainly found: a) along coastal lowlands and alluvial plains of major rivers, areas suitable for industrial development; b) in intermediate zone of undulating hills with favourable conditions for agriculture; and c) at the mountainous interior where minority of indigenous groups reside [2].

Since the 1800s, the world has been fascinated by Sarawak's remote jungles, its wildlife and tales of head-hunting tribes from adventure stories by early modern travellers. James Brooke (1803-1868) the English adventurer and an amateur naturalist, became the first Rajah of Sarawak in 1841. Alfred Russel Wallace (1823-1913), co-discoverer of evolution by natural selection with Charles Darwin, made important discoveries on evolutionary biogeography while in Sarawak in the 1850s [5] (as a guest of Rajah Brooke). Influenced by Wallace, William T. Hornaday (1854-1937), the American taxidermist and later an advocate for wildlife protection laws, came to Sarawak in the 1870s [6] to collect museum specimens of large animals including orangutans [7].

The fascination and early ideas about orangutans in the West began as early as the 17th century. The earliest mention of "Ourang Outang" or 'man of the forest' were by the Dutch physicians Jacobus Bontius (1592-1631) working in Java [8] in 1631 and Nicolaes Tulp (1593-1674) in his widely read essay entitled "*Homo sylvestris*; Ourang-Outang" in 1641 [9]. Subsequently, popular debates on human evolution after the publication of Darwin's theories sparked an increased demand for the red apes as specimens and museum exhibits in Europe [10].

The Sarawak Government under the Brooke rule limited the number of orangutans hunted and collected in the wild. The Rajah made the decree at least prior to 1909 as demand for the red apes increased in the West [11]. Bruen & Haile reported that over 200 orangutans were hunted and exported out of Sarawak by the early 1900s [12]. In 1960, a global estimate by

Zoological Society of London showed that at least 248 orangutans were in captivity in zoos worldwide [13]. Harrisson [13] estimated approximately 125 orangutans were in captivity in private hands across Southeast Asia during the 1950s. To put into perspective, Schaller [14] estimated that orangutan populations were between 450 and 700 animals at known orangutan habitats in Sarawak at the time of his study in 1961.

Sarawak began responding to attempts to conserve landscapes including for orangutan habitats since the late 1930s. The Forest Department's policy of only allowing logging operations in 'areas with sufficient stock for regeneration' limited operations between 1933 to 1962 [15]. The *Maias Protection Commission* set up in 1959 identified Sedilu, Sebuyau and Simunjan as reserves for orangutan protection [12]. The first protected area, Lanjak-Entimau Protected Forest was initially constituted in 1938 against shifting cultivation or slash-and-burn agriculture, not for orangutan conservation [16]. In 1983, the Sarawak Government (after the formation of Malaysia) gazetted the 168,758 ha Lanjak-Entimau landscape as a Wildlife Sanctuary for orangutans and followed this up with the gazettement of its sister park, the Batang Ai National Park (24,040 ha) in 1991.

In 1996, the Sarawak Legislative Assembly unanimously approved the policy document 'A Master Plan for Wildlife in Sarawak'. The Master Plan was formulated by a Special Select Committee and included recommendations that were subsequently adopted by the Sarawak Government. Among the notable changes made were: 1) the creation of the streamlined National Parks and Nature Reserves Ordinance (1998) and the Wild Life Protection Ordinance (1998); 2) stronger staff capacity building; 3) better field enforcement, control over sale of guns and ammunition; 4) ban on commercial sale of wildlife, and; 5) more proposals to create more protected areas for wildlife, including orangutans [17,18]. The Forest Department's National Parks and Wildlife Division then was tasked to manage the totally protected areas (TPAs) between 1991 and 2003.

In 2003, the Sarawak Government legalized a corporate entity named Sarawak Forestry Corporation (SFC) to be the Forest Department's operating arm in managing protected areas and biodiversity conservation in the State. SFC initially brought with it a business philosophy with key performance indicators as measures of profitability for the corporation [19]. This led to management changes which included greater emphasis on reducing losses and numbers of park staff, as well as reduction in community conservation and communications in TPAs including at Batang Ai National Park. The changes led to general unhappiness among the privileged communities as well as reduced commitment to protect conservation targets by park authorities, thus minimal control over illegal hunting and encroachment into TPAs at the time.

By the 2010s, there were multi-agency efforts to: a) conserve orangutans in Sarawak; b) address the livelihoods of affected communities living around orangutan habitats; and c) clarify agency roles and jurisdictions. Among the outputs include at least three management plans drafted as guidelines for implementing agencies to address the above points [18,20,21]. The main highlight at this stage was the Government's pledge to have zero-loss of orangutans and their habitats in the State [22]. The late Chief Minister of Sarawak, Adenan Satem affectionately known as Tok Nan (1944-2017) made the public pledge in 2015. Tok Nan's intense efforts to conserve orangutans and to expand protected areas for the critically endangered species permanently marked his conservation legacy in Sarawak after his death.

Thesis structure

This MPhil thesis is presented in five chapters. I have briefly introduced the historical context of orangutan conservation in Sarawak in the first section of this chapter. To continue the narrative, the first step of the present conservation efforts is to acquire baseline data on population estimates and distribution at the core habitats of Batang Ai-Lanjak-Entimau (BALE), where most of the viable orangutan populations are found. A Government policy for orangutans in Sarawak was drafted, but yet to be tabled and signed off as official policy at the Sarawak State Cabinet. If approved, collaboration is anticipated between conservation partners and government agencies to implement the policy recommendations. The purpose of this MPhil thesis then is to provide a comprehensive and updated report on orangutan conservation for the intended joint collaborators.

In Chapter 2, my co-authors and I provide a review on the threats to orangutan survival and lessons learned from past conservation strategies in Sarawak. The two biggest threats to orangutan survival are habitat degradation and forest loss, and hunting. Subsequently in 2016, the threat level for Bornean orangutans was upgraded to 'Critically Endangered' under the IUCN Red List of Threatened Species. We discuss the measures taken to protect orangutans in Sarawak as well as the shortfalls of conservation responses in the past 60 years. We include four recommendations from the lessons learned, which range from inter-agency collaborations, new technological application, alternative community livelihood development, to increased public support for conservation policies.

Chapter 3 is the first of two chapters where my co-authors and I present research findings based on unpublished data provided by the Wildlife Conservation Society (WCS) Malaysia. In Chapter 3, we show in detail the steps to generate precise and reliable population estimates of orangutans at the core habitats of BALE Landscape. This is done by integrating Bayesian analysis into existing great ape survey methods, that is the Marked Nest Count method. We also discuss the limitations and advantages of the study design as well as recommendations to improve the sampling scheme.

Chapter 4 continues the research findings with an academic exercise in mapping orangutan distribution using occupancy modelling based on the unpublished data by WCS Malaysia. We show how the model uses survey records of new orangutan nests as proxies to generate maps of occupancy probabilities and their degrees of uncertainty. We then discuss recommendations to fine-tune the study design for potential re-surveys at the study sites and/or for future surveys at sites outside the core orangutan habitats.

Finally, I reflect in Chapter 5 my MPhil findings, the growing science, and the way forward for orangutan conservation in Sarawak. I discuss the contribution of the studies conducted in this MPhil thesis, the limitations and lessons learned from them, as well as the direction and potential for future collaborations. I conclude by describing how WCS Malaysia could apply the research findings into its orangutan conservation projects not just at the BALE Landscape, but at other focal sites with remnant orangutan population outside the core habitats in Sarawak.

Chapter 2.

Threats and lessons learned from past orangutan conservation strategies in Sarawak, Malaysia[a]

Joshua Pandong[b,c], Melvin Gumal[b], Zolkipli Mohamad Aton[d], Mohd. Shahbudin Sabki[e], and Lian Pin Koh[c,f]

2.1. Abstract

In 2015, the Sarawak Government made a public pledge to stop illegal logging in the State, to create more national parks, and to move towards a zero-loss policy of orangutans and their habitats in Sarawak. Conservationists welcomed this policy in view that threat level for the Bornean orangutans under the IUCN Red List has been upgraded to Critically Endangered in 2016. The main threats to orangutan survival include habitat degradation and forest loss which is rapidly driven by large-scale development of unsustainable land-use change. The cultural taboo against orangutan hunting is slowly eroding with evidence of the species being killed in vulnerable areas. We discussed shortfalls of conservation responses in the past 60 years in Sarawak which included unknown rate of illegal orangutan killings, inadequate law enforcement, and incomprehensive community development strategies. The recommendations to address these shortfalls then include: a) inter-agency collaboration for orangutan population monitoring, b) technological application and intelligence networks to intensify enforcement strategies, c) alternative community livelihood development and self-enforcement, and d) increased public support for conservation policies. The implementation of the zero-loss policy is anticipated to emphasize the needs for orangutan protection amid rapid development plans around critical habitats.

Keywords: Bornean orangutans, community livelihood, government policy, hunting, law enforcement, Sarawak.

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2.2. The global status of Bornean orangutans

The orangutan (*Pongo* spp.) is the largest and most charismatic ape in Asia. Historically, they ranged from the foothills of the Himalaya to the Sunda islands of Sumatra, Borneo and Java, covering a distribution area of 150 million ha [1,2]. In the 17th century, records by early European explorers found their range size to be only on the islands of Borneo and Sumatra [3,4]. At present, their geographical range sizes are 21% and 2.3% of the island landmasses respectively [5-7].

It was only in the past 15-20 years that the scientific community recognized orangutans on the two islands as different species, *Pongo pygmaeus* in Borneo and *Pongo abelii* in Sumatra (north of Lake Toba) [8-10]. In 2017, a third species named *Pongo tapanuliensis* (south of Lake Toba) was described [11]. The Bornean species *P. pygmaeus* is divided into three subspecies, *P. p. morio*, *P. p. pygmaeus* and *P. p. wurmbii* [5,9,12].

The three Bornean subspecies are distributed across 42 geographically distinct population and metapopulation units [13]. *P. p. morio* are found in larger numbers in the Malaysian state of Sabah, with smaller populations in the Indonesian province of East Kalimantan. *P. p. pygmaeus* is found mainly in the Batang Ai-Lanjak Entimau (BALE) Landscape of the Malaysian state of Sarawak as well as in Betung Kerihun and Danau Sentarum in the Indonesian province of West Kalimantan. *P. p. wurmbii* occurs mainly in the Indonesian province of Central Kalimantan [14,15].

A habitat suitability study by Struebig et al [16] estimated an approximate loss of up to 24% or 7 million ha of core orangutan range between the 1950s and 2010. Given continued land cover and climate changes, the study forecasted core range habitat loss to be at 74% or 23.3 million ha between 2010 and 2080 for Borneo [16]. The island lost 30.2% or 16.85 million ha of forest area to logging, fire and large-scale land-use conversion into plantations between 1973 and 2010 [17]. In Sabah and Sarawak, only 22% or 4.2 million ha of land surface remained as intact forest (unlogged) at the end period between 1990 and 2009 [18].

Habitat fragmentation and the extremely low reproduction rate of orangutans exacerbated the decline further [19]. The internal Population Viability Assessment (PVA) report in 2016 found smaller meta-populations of orangutans in West and Central Kalimantan being most severely impacted by human activities including industrial agriculture (oil palm plantations) and poaching [13]. The study also found that populations with ≤300 orangutans will suffer 86%-90% decline in 100 years if removal of adults persists. The extinction rate is even faster if habitat loss due to large-scale land-use change is taken into account [20].

In 2016, the International Union for Conservation of Nature (IUCN) upgraded the threat level for Bornean orangutans to ‘Critically Endangered’ under the Red List of Threatened Species [5]. The upgrade was made in view of the escalating threats and rapid population decline documented over the span of three generations, or about 75 years. The urgent review was prompted by the precautionary approach formulated in Principle 15 of the Rio Declaration 1992, ‘where there are threats of serious or irreversible damage, the lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation’ [21], that is to prevent further decline of orangutan population. The two main goals of conservation are to: a) maintain habitats and improve connectivity; and b) fight illegal hunting and killing of this protected species (as hunting is a major extinction force in most parts of the species range) [13].

The Indonesian and Malaysian Government agencies and relevant stakeholders formulated long-term action plans for orangutan conservation in Borneo. These official documents include: a) *Orangutan Indonesia: Conservation Strategies and Action Plan 2007-2017* [22]; b) *A Master Plan for Wildlife in Sarawak* [23]; c) *Orangutan Strategic Action Plan: Trans-boundary Biodiversity Conservation Area 2010-2020* for the Batang Ai-Lanjak-Entimau-Betung Kerihun Landscape of Sarawak and West Kalimantan [24]; d) *Sabah Orangutan Action Plan 2012-2016* [25]; and e) *Ulu Sungai Menyang Orangutan Strategic Action Plan* for the non-protected conservation area next to the BALE Landscape (Forest Department Sarawak & Wildlife Conservation Society (WCS) Malaysia, unpublished).

The action plans for orangutan conservation have been difficult to implement without the full commitment from the governing authorities on a zero-orangutan loss policy. In 2015, the Sarawak Government made a public pledge to stop illegal logging in the State, to create more national parks, and to move towards a zero-loss policy of orangutans and their habitats in Sarawak [26]. However, only effective collaboration between the government, conservation practitioners, research institutions, rural communities and the corporate sector can ensure the success of such crucial policy [27,28].

In this chapter, the authors highlight the threats to orangutans and the implementation of overlapping conservation strategies within the Sarawak context. This is in line with a greater accountability and openness approach adapted by the Sarawak Government since May 2018. A review of the conservation strategies in Sarawak is necessary in view of the continuous decline of this protected species. Furthermore, there are suggestions for greater accountability for the environment in Malaysia [29]. This chapter serves as the backdrop for ongoing and upcoming collaboration between the Sarawak Government, their conservation partners and various stakeholders in moving towards a policy of zero-losses for orangutans and their habitats.

2.3. Pressures on Bornean orangutans

Two of the biggest threats to the survival of large-bodied mammals in Southeast Asia have been habitat loss and intensive hunting [30-33]. Sodhi et al highlighted the conservation importance of Southeast Asia as being one of the highest regions for species endemism, yet also the highest for biodiversity loss and annual deforestation rate in the tropics [34]. These factors have been attributed to the extinction in the wild of Javan rhinoceros (*Rhinoceros sondaicus annamiticus*) in Vietnam in 2010 [33], and the Bornean rhinoceros, one of the subspecies of the Sumatran rhinoceros (*Dicerorhinus sumatrensis harrissoni*) in Sabah in 2015 [35]. The extinction process also threatens the orangutans in Sumatra. Two of the great ape species that could soon become extinct are the Sumatran (*P. abelii*) and Tapanuli orangutans (*P. tapanuliensis*). At an annual rate of 10-15% in habitat loss due to logging, both species are the most vulnerable to extinction possibly in the next 50-100 years [11,14,32].

The internal 2016 PVA analysis of the *P. p. pygmaeus* populations in six habitat units in West Kalimantan and Sarawak have shown that they are sufficiently large to support ‘demographically and genetically healthy populations’ in the joint landscapes of Batang Ai-Lanjak-Entimau-Betung Kerihun [13]. However, *P. p. pygmaeus* is estimated to have the lowest number of individuals among the three Bornean subspecies with an estimated population of 3,500 orangutans [5,13]. Identifying the direct threats to the species survival is a crucial step in achieving the goal of conserving and sustaining the orangutan population in Sarawak.

2.3.1. Habitat degradation and forest loss

The two main activities that drive habitat degradation and forest loss in Sarawak are logging and large-scale land-use conversion into plantation [17-19,36].

2.3.1.1. Logging

Past studies have shown that road access in logging concessions increased overhunting of wildlife and endangered mammals, fuelled market demand for wildlife, as well as reduced the long term sustainability of the harvested populations [37,38]. In Borneo, Sarawak has the highest density of logging roads amongst the states or provinces on the island (average for Borneo: 0.48 km km^{-2}, and for Sarawak: 0.89 km km^{-2}) [17]. The road networks expanded as log production steadily climbed in the late 1970s and peaked in 1991 with over 19 million m^3 harvested [39] before declining to about 9.6 million m^3 by 2011 [40]. A total length of 82,239 km (out of 271,819 km in Borneo) of primary logging roads was built between 1973 and 2010 in Sarawak [17]. In Sabah, orangutans were found to be able to cope in areas with sustainable logging practices using the reduced impact logging (RIL) but not in areas with heavy extraction due to conventional logging [41,42]. These studies show that logging became a threat when food resources were destroyed and when resident orangutans were displaced and moved towards non-disturbed areas that were not suitable orangutan habitat.

2.3.1.2. Large-scale land-use conversion into plantation

The increase in logging operations in Sarawak was also followed by oil palm and forest plantation expansion in the State. In 1980, only 23,000 ha of land were planted with oil palm in Sarawak compared to 1.56 million ha in 2017 [43]. By 2017, Sarawak became the largest oil palm planted state at 26.8% of the total oil palm planted area in Malaysia, followed by Sabah (26.6%) and Peninsular Malaysia (46.6% for the 11 West Malaysian states combined). The combined export earnings from palm oil products in Malaysia was valued at MYR77.85 billion (~USD19 billion) in 2017, that is an increase from MYR67.92 billion (~USD16.6 billion) in 2016. The revenue from the palm oil industry is thus one of the largest sources of revenue for Sarawak and Malaysia in 2017 [43].

Industrial forest plantation has progressed in Sarawak for over three decades with acacia (*Acacia mangium*) as the preferred species for plantations in view of its fast-growing performance as well as flexibility to grow on poor and degraded soils [39,44]. Acacia is harvestable after seven years with a survival rate of 50-60% and reported to yield volumes between 150-170 m^3 ha^{-1} [44]. In 2018, Sarawak has the largest area of planted forests (mainly of acacia) at 403,017 ha, followed by Sabah (300,521 ha) and Peninsular Malaysia (113,112 ha) [44]. The total export volume of acacia for Sarawak in 2017 was 1.1 million m^3, which was valued at MYR203 million (~USD49.6 million) [45].

At present, the proportion of orangutan range impacted by the development of both commodities (oil palm and planted forest) in Sarawak is unknown. Orangutan ranges in Sarawak are mostly surrounded by homogeneous plantations and forests exploited for timber [24]. Surveys are in the works to determine the survival rate of the great apes in the plantations and concession areas (JP & MG, pers. obs.). In Sabah, orangutans have been observed to use various human-transformed landscapes for nesting and feeding, albeit the plantations were noted to be incompatible with viable populations [46]. In East Kalimantan, the orangutans were also observed at planted forests intermixed with highly degraded forests and scrublands, but their long-term viability there remains unclear [42].

2.3.2. Hunting

Humans have hunted orangutans for the past 35,000 years [47,48]. Archaeological records of charred orangutan bones in Sarawak's Niah Cave in the 1950s were consistent with human predation for food [49]. Between the 1860s and 1900s in Borneo, almost 300 orangutans were extracted from the wild by a list of collectors or hunters including notable naturalist such as Alfred Russel Wallace [50-54]. The increased demand for the red ape as specimens and museum exhibits in Europe was sparked by popular debates on evolution after the publication of Darwin's theories at the time [3]. Zoo collections were also seen as the 'science' of that generation.

The results of the Kalimantan-wide interview-based survey on orangutan conflicts and killings published in 2011 were alarming. The rates of orangutans being killed far exceeded the maximum productivity for viable populations in Kalimantan [55]. It was discovered that out of the respondents reported to have killed orangutans (n = 143 respondents), 56% did so for non-conflict reasons, that is for food than for conflict reasons such as out of fear or in self-defence [56]. The frequency of killings was the most severe in areas with large orangutan populations and high rates of land-use conversion from natural forest into plantations [31].

In Sarawak, there is no similar knowledge or surveys on hunting of orangutans, apart from random reports in the mid-2000s and 2010s. There is however a large-scale documentation of general hunting and wildlife trade in the period before. In the mid-1980s, legal gun ownership exceeded 60,000 registered shotguns with 2 million cartridges fired annually [57]. By the 1990s, subsistence hunters harvested at least 23,513 tons of wild meat per year with 80% of this consisting of three ungulate species namely bearded pig (*Sus barbatus*), Sambar deer (*Cervus unicolor*) and barking deer (*Muntiacus muntjak*) [37]. The market value of wild meat consumption by rural people at the time was estimated at USD75 million per year [58]. The effects of overhunting and commercial wildlife trade were documented and its effect included decreases in population size, average body size, older age classes, annual production and local extinction in heavily hunted sites [37].

2.3.3. Vulnerable orangutan populations

Currently, the Sedilu-Sebuyau-Lesong Landscape is the only known remnant orangutan population outside (or 120 km to the west of) the protected Batang Ai-Lanjak-Entimau (BALE) Landscape in Sarawak (Fig. 2.1) [59,60]. Sedilu-Sebuyau-Lesong is a fragmented conservation landscape that consists of three separate national parks. These parks are close to each other, with Lesong being less than 2 km away from the southern boundary of Sebuyau. At present, the peat swamps surrounding this landscape is under threat of conversion into oil palm plantation. Between 2011 and 2016, at least two infant pet orangutans from Lingga (an area outside the Ulu Sebuyau National Park) were rescued, as informed by the Park Warden of Matang Wildlife Centre, Kuching (S. Aban, pers. comm.). It is unknown if the rescued infants were part of orangutan pet trade in Sarawak; but if illegal trade is occurring, the impact even in small numbers is huge given the low breeding rate of the species [61].

2.4. Extending protected areas as a conservation response in Sarawak

Among the first documented responses to conserve orangutans in Sarawak was the formation of the *Maias Protection Commission* by the then colonial Government of Sarawak in 1959 [59,62]. The Commission was set up to mainly inquire into the constitution of a wildlife sanctuary at the Sedilu, Sebuyau and Simunjan reserves for orangutan protection. The response was driven by the continued decline of the species population due to rapid development, increasing human population, and collection of orangutans for overseas zoos and institutions at the time [62].

Schaller (1961) followed up the *Maias Protection Commission*'s findings by conducting the first surveys in Sarawak or Sabah. He used orangutan nest counts as a proxy to direct detections of orangutans [60]. The collaboration consisted of the Sarawak Forest Department, Sarawak Museum and Wildlife Conservation Society (then known as New York Zoological Society). Schaller reported about 450-700 orangutans in Sarawak at the time. However, the population estimate was limited to the then known distributional records. He also made recommendations to protect continuous tracts of primary forest for the survival of small orangutan populations.

Since the 1980s, the Sarawak Government has set aside more than 200,000 ha of forest for orangutan conservation. This include the Lanjak-Entimau Wildlife Sanctuary (168,758 ha) and Batang Ai National Park (24,040 ha) in 1983 and 1991 respectively. Subsequent gazettement of National Parks for orangutan conservation were Sedilu National Park (5,970 ha), Ulu Sebuyau National Park (18,287 ha) and Gunung Lesong National Park (595 ha) in the 2010s. The Sarawak Government in 2015 has reaffirmed its commitment to conserve orangutans especially by creating huge area of forest as orangutan reserves. The late Chief Minister of Sarawak, Adenan Satem in 2015 pledged to stop illegal logging in the State, to create more national parks, and to move towards zero-losses of orangutans and their habitat [26]. This pledge is still maintained as State policy by his successor and the current Chief Minister, Abang Johari Tun Openg (MG, pers. obs.).

Since 2011, orangutans have been documented in non-protected areas outside existing national parks and wildlife sanctuaries. These include (a) the Ulu Sungai Menyang landscape (14,000 ha) which is contiguous to the Batang Ai National Park, and (b) the proposed Sebuyau-Lesong connector (up to 711 ha) [13,63]. Presently, the Sarawak Government has proposed Ulu Sungai Menyang as a Conservation Area with High Conservation Value Forest (HCVF), as this has a globally significant orangutan population [64]. There are also proposals to assign a legal protection status for the proposed Sebuyau-Lesong connector, the proposed Sebuyau-Sedilu connector (up to 1,618 ha), and the proposed Sebuyau extension (up to 3,169 ha) (Fig. 2.1). If gazetted, these areas will provide wider forest connectivity for foraging and prevent further habitat fragmentation of orangutan habitats.

Presently, WCS Malaysia is conducting orangutan population and distribution studies at all sites with orangutans in Sarawak. Findings to date include an estimated 1,175 to 2,582 orangutans in Sarawak [64]. However, this estimate is credible only if the whole BALE was homogenous and consisted of ridges. Rapid assessments of orangutan nest are still ongoing at three other areas adjoining Sarawak and Kalimantan, with the objective of verifying reports of orangutan sightings there in the past 10 years. Social surveys are also ongoing at villages located within 5 km of WCS orangutan study sites. The objective is to acquire baseline data on community perceptions towards wildlife and protected areas. This is in line with the State Government's long-term plans to introduce strategic collaborations to gain more community involvement in conservation and tourism in areas with natural orangutan habitat [65].

2.5. Shortfalls in orangutan conservation responses in Sarawak

There is still a need to address notable shortfalls for orangutan conservation in the State despite the positive efforts by the Sarawak Government to gazette more areas as national parks and propose areas with legal protection status under Section 28 of the Wild Life Protection Ordinance (WPO) 1998 for orangutan conservation.

2.5.1. Hunting persists at an unknown rate

To date, a current field-based scientific survey of orangutan killing is unknown in Sarawak, although an estimate exists for Borneo [19,36]. Voigt et al [36] used geographic information system (GIS)-based analyses of losses of suitable orangutan habitat from 1999 to 2015 to generate an estimate of orangutan decline in Borneo. Voigt et al's GIS-based study postulated that the total loss in Sarawak was estimated at 900 individuals in 16 years with 95% confidence interval of 250 to 1,600 individuals. The methodology used by Voigt et al could have been improved further if areas not occupied by orangutans are excluded from the analyses, even though it was deemed suitable habitats for the species (JP & MG, pers. obs.). Another analysis led by Santika et al indicated a similar alarming decline of 22.2% for orangutan population per 10,000 ha between 1997 and 2015 in Sarawak, and 25.3% in Borneo [19].

The cultural taboo against hunting orangutans and the respect for the total ban of hunting totally protected species under WPO1998 [58] is on a decline. There were reports and evidence of orangutans being killed on at least three occasions in Sarawak. In 2004, four carcasses were seen by WCS field teams and two were allegedly close to a longhouse [66]; in 2012, a male orangutan was discovered with its skin removed outside the Ulu Katibas extension to the Lanjak-Entimau Wildlife Sanctuary, a WCS study area at the time (S. Ajom, pers. comm.); in 2016, the carcass of a flanged male orangutan with gunshot wounds was discovered at the proposed northern extension of Batang Ai National Park (B. Chendai, pers. comm.). The local communities living around the Batang Ai-Lanjak-Entimau (BALE) Landscape traditionally do not hunt orangutan [59,67]. It is culturally prohibited to hunt as the Ibans believed their ancestors were reincarnated as orangutans in the past and they were called to co-exist [68].

2.5.2. Inadequate law enforcement

Before 2018, law enforcement of wildlife crime in Sarawak is a complicated process due to overlap of jurisdictions between two enforcement agencies, namely: (a) the State Government's Forest Department Sarawak (FDS), and (b) the Sarawak Forestry Corporation (SFC), a corporate entity formed in 2003 to be FDS' operational or implementation arm. SFC's Protected Areas and Biodiversity Conservation unit (PABC) legally manages totally protected areas (TPAs) in Sarawak and enforces provisions under the various laws and ordinances pertaining to wildlife within TPAs. FDS had also been mandated to enforce laws pertaining to wildlife. However, legal power to investigate offenses committed under the same laws and ordinances resides only with FDS.

These roles and the switching of the mandated enforcement agencies (in the intervening period between 2003 to 2018) has led to a perceived lack of coordination on which implementing agency is mandated to enforce the laws in Sarawak. In comparison, various partners with well-defined roles managed to jointly conduct over 10,000 km of patrols in the states of Johor and Pahang in Peninsular Malaysia in 2011 [69].

Previously, SFC indicated that lack of funding, training and manpower to conduct ground patrols and aerial orangutan surveys were reasons for inadequate law enforcement, especially at the core orangutan habitat of the BALE Landscape. The cost of patrolling at the BALE Landscape was quite expensive and each patrol could cost between MYR8,000 and

MYR12,000 (USD1,950 to USD2,930) including the cost of allowances and logistics [24]. SFC conducted quarterly patrols and there were at least four SFC personnel assigned per trip.

Other reasons for the lack of enforcement at the BALE Landscape include community objections towards the perceived ownership of the protected areas by SFC. The community is reluctant to collaborate in joint patrols as field guides or assistants as there was a perceived view that SFC is a corporate entity and thus was focussed on reducing losses, making profit, and increasing efficiency. The perceived view by the communities was also because of: (a) reduced the numbers of park staff at Batang Ai National Park and Lanjak-Entimau Wildlife Sanctuary; (b) removal of the staff/village rotation system of hiring local communities, and (c) less permanent and contract staff to work at the park [66].

2.5.3. Incomprehensive community development strategies

The dissent by some of the local communities around the BALE Landscape towards SFC and FDS was compounded by the lack of road infrastructure and economic development due to the protected area status at the Landscape. In 2013, WCS Malaysia showed that 22.15% (*n* = 334) of the respondents interviewed from 27 randomly selected villages around the Landscape perceived that the protected areas provided no employment and economic opportunities to their households. The main sources of income for the villagers were farming and fishing. This is in line with the findings that the younger generation of Ibans are migrating out of rural villages into urban areas to look for stable jobs, leaving behind an aging farming population [70]. Some others were employed by local tour operators but only around the Batang Ai National Park.

In many parts of Sarawak, the main economic development perceived to be profitable by the local communities is conversion of their lands into oil palm plantations. Currently, there are two categories of oil palm plantation as defined by the Department of Agriculture: smallholders and large-scale estates [71]. The Sarawak's Ministry of Modernisation of Agriculture, Native Land and Regional Development (MANRED) projected an expansion rate at 10% per year for plantation development. As most State Lands are being developed, there has been a shift towards persuading smallholders who own Native Customary Rights (NCR) lands to convert their land-use into oil palm. The area size of plantations owned by smallholders have since grown from 95,700 ha in 2013 [72], and is expected to reach 380,000 ha by 2020 [71]. NCR lands, as defined by the Sarawak Land Code (1958), refer to the 'untitled land held by license from the State, primarily on the basis that it had been cultivated by traditional means before 1958'.

Since the 1950s, local communities were often not in favour to give up their NCR lands for a National Park status for fear of 'losing their land' or losing 'access to a traditional resource'. As such, most of the protected areas have caveats that allow communities access to the protected areas or to retain their NCR status. Lands are considered invaluable to local communities. This is especially so now, as there are economic opportunities to earn income from these areas. Nevertheless, there are however some communities that are in favour of retaining forests in their NCR lands and these tend to be ones that can eke out some economic value from their NCR lands, such as via tourism.

2.6. Successes of recent initiatives: Lessons learned and recommendations

An adaptive management of conservation actions in response to new knowledge is a critical part of effective conservation practice to protect orangutans in Sarawak. We recommend the following:

2.6.1. Inter-agency collaboration for adequate enforcement and orangutan population monitoring

Joint patrols by various authorities with technical support from conservation partners with local knowledge can be an efficient form of focussed enforcement at the BALE Landscape. This is evident with the successful arrest and prosecution of six illegal trespassers from Indonesia in April 2018. The stint in March 2018 was in collaboration between SFC as the patrol leader, Royal Malaysian Police, Armed Forces and WCS Malaysia, as well as FDS as the lead investigator after the arrest. The success was partly due to an improved coordination between the agencies after several joint trainings. These include: (a) the *Law and Enforcement Techniques* workshops jointly organized by SFC and WCS Malaysia for SFC rangers and Honorary Wildlife Rangers since 2013; and (b) the *Prosecuting Wildlife Crimes and Advocacy* workshop by the Sarawak State Attorney-General's Chambers with participation from eight departments and non-governmental organizations (NGOs) in November 2017.

Conservation partners led by FDS previously conducted joint efforts under the Heart of Borneo (HoB) Initiative for orangutan monitoring in Sarawak. The HoB Initiative is a voluntary transboundary cooperation between Malaysia, Indonesia and Brunei Darussalam, with the "protection of forest, maintenance of vital ecological functions, cultural survival, and alleviation of poverty" as its main objectives [73]. The large-scale expeditions involving five organizations confirmed sightings of orangutan nests and direct observations at the non-protected landscapes of Ulu Sungai Menyang (south of BALE) in 2012 and 2013, Engkari-Telaus (west of BALE) in 2014, and Pasin Concession Area (east of BALE) in 2015. Based on an internal FDS memo, these areas are no longer timber concessions after FDS rejected the applications for license renewal upon the discovery of orangutans during the expeditions there.

We recommend the continued inter-agency collaboration for enforcement and regular orangutan population monitoring in view of the recent success of improved agency coordination. In-kind contribution from participating agencies will compensate for the limited funding and manpower, whilst joint trainings and experience exchange is anticipated to improve patrol quality. At present, up to 18 joint enforcement patrols are conducted each year at BALE Landscape with plans to increase the frequency and efficiency using the Spatial Monitoring and Reporting Tool (SMART) approach (http://smartconservationtools.org/) (ZMA & MG, pers. obs.). Enforcement support is further detailed in the next section.

2.6.2. Corresponding support through technological application and intelligence networks

All joint patrols by SFC and WCS Malaysia since 2017 were based on the SMART approach [74]. SMART is a GIS-based tool developed to combine standardized patrol data collection, site-based database management, planning, decision-making and evaluation. The aim is to provide managers with easy access to information to facilitate best practices for protection and capacity building at the landscape of interest [74]. Enforcement based on a SMART approach can eliminate the need for additional paperwork and data processing after patrol completion. The internet of things (IoT) has enabled the ability to collect and interpret data in real-time as people and things are connected via multiple smart devices [74].

SMART patrols are also implemented for ongoing village anti-poaching patrols supported by WCS Malaysia at the Ulu Sungai Menyang and Ulu Engkari areas, which are contiguous to the Batang Ai National Park. In unpublished reports, WCS Malaysia highlighted that despite the objection towards protected areas, respondents replied that illegal encroachment into their own NCR lands was a security and priority threat. The highest score at 32.34% (*n* = 334) to the question of the responsibility of the longhouse community was the collective response 'to work together between communities to control illegal activities committed by outsiders by enforcing communal laws on the offenders'. Thus, the patrols commenced in November 2017 were aimed to provide and equip local communities to take the lead in safeguarding their lands, which consequently make them the gatekeepers of the protected areas.

SFC has invested in drone technology and drone pilot training for its forest management activities since 2015 [75]. Drones come in various shapes, sizes and functionalities; and have become increasingly appealing for being flexible, low-cost and extremely useful to acquire high-resolution imagery. The unmanned aerial systems (UAS) have been instrumental in filling data gaps and supplementing manned aircraft and satellite imagery for a wider and more detailed coverage. Although drone visibility is limited to open areas, variant cameras or scanners developed for remote sensing could potentially be used to penetrate through closed forest canopy [76]. This is vital even at this experimental stage as the undulating regions in the interior Sarawak are difficult to access.

We recommend the continued multi-agency collaboration to invest and train rangers, park managers and decision makers using the SMART approach. The trainings are expected to harness the IoT via the emerging developments in computing and communication technologies. In addition, we recommend the continued long-term presence and interactions at the villages around BALE Landscape which helps to rebuild trust between the agencies and the resident communities. This is evident by the tip off leading to the arrest and prosecution for the case discussed in the previous section. The enforcement authorities are recommended to make full use of their resources for targeted patrols with the local communities being their eyes and ears on the ground. A mechanism is being proposed to reward informants for intelligence leading to successful arrest and prosecution. This is vital not only to maintain a positive working relationship with the resident communities, but a cost-effective measure to increase enforcement successes.

2.6.3. Alternative community livelihood development

The Sarawak Government heeded the community objection against the creation or expansion of protected areas for orangutan conservation in view of the NCR land disputes. The next best option is the proposed implementation of Section 28 of the WPO1998. This Section does not infringe the rights of NCR land owners as the main objective of the Minister's Order is to prohibit large-scale conversion of land-use for commercial purposes. A list of prescribed activities will be agreed upon first between the State Government and the local communities before gazettement. The first draft of a State Cabinet paper was prepared in June 2017 and is currently under revision to clarify agency roles stipulated in the manuscript (MSS & MG, pers. obs.).

Meanwhile, FDS have begun to implement their community livelihood programs in Ulu Sungai Menyang as part of empowering the villages to be more self-sustaining. Among the ongoing projects since 2017 include: (a) small-scale gaharu plantation to supply gaharu tea leaves; (b) *bemban* (a rattan species) planting for handicraft supplies; (c) handicraft carnivals to market goods made from non-timber forest products (NTFP); (d) skill-based workshops on boat and outboard engine repairs, as well as fibre glass boat construction and maintenance; (e) free, prior, informed consent (FPIC) workshop with participation from local communities; and (f) joint micro-hydro dam projects with Universiti Malaysia Sarawak (UNIMAS).

We recommend the continued development of joint projects as it has the potential of building a sense of ownership towards wildlife and protected areas by the resident communities. The target areas are sites with conservation interest for orangutans in Sarawak. The objective of these projects is then to instil in all the communities, a long-term sense of ownership for orangutans and their habitats.

2.6.4. Increased public support for conservation policies

The long-term action plans for orangutan conservation developed for Sarawak are subject to review upon completion of their implementation stages. This include the comprehensive Master Plan for Wildlife in Sarawak developed in 1996. A revision and update of this document and policies is being finalised. Meanwhile, the proposal to implement Section 28 of WPO1998 and grant legal protection status for sites with orangutans is being examined.

There is a pressing need to increase public support for the implementation of conservation policies by the government. The de-emphasis of environmental value over economic development by the new Malaysian Federal Government is worrying [77]. The overall environmental health and ecosystem vitality in Malaysia is already on an alarming and decreasing trend with the drop in the National Environmental Performance Index (EPI) score of 83.3% in 2006 [78] to 59.22% in 2018 [79].

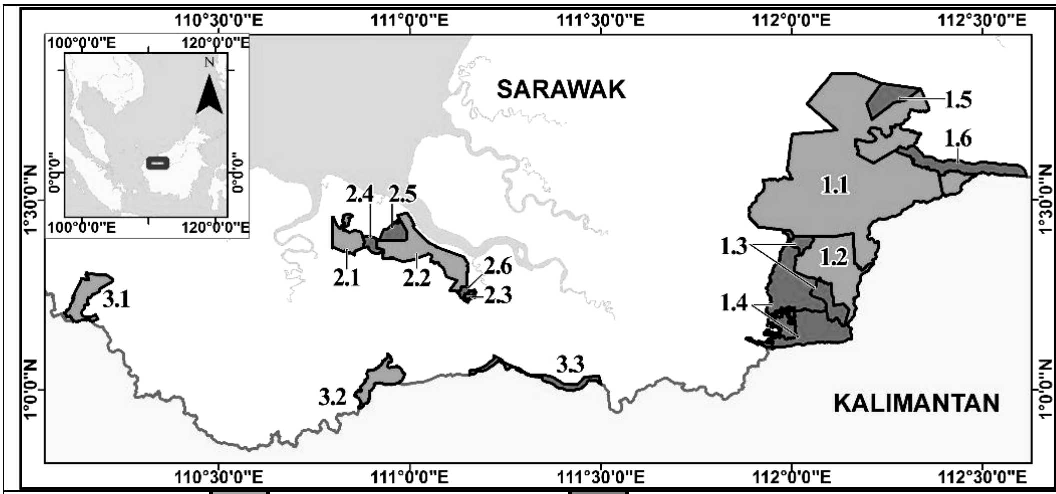
We recommend conservation partners to jointly conduct public events to increase civic awareness on environmental issues with emphasis on species conservation including orangutans. The desired outcome of the public events may not be immediate and the indicators to measure impacts may still be disputed. But the need is urgent, as it allows for conservation partners to engage the wider society as well as to rally support to influence policy makers in tabling responsible and sustainable environmental policies along with the Government's economic development.

2.7. Conclusion

This perspective chapter highlights that the Bornean orangutans in Sarawak are under threat by habitat degradation and forest loss as well as hunting despite the Sarawak Government's efforts to increase more lands for protection and endorse strategic action plans for orangutan conservation since the 1980s. The inadequate law enforcement and incomprehensive community development strategies in and around the core orangutan habitat of BALE Landscape led to adaptive actions taken to counter these indirect threats.

The best set of actions for orangutan conservation to date is the inter-agency collaboration for enforcement, orangutan monitoring of its current distribution and surveys to estimate their populations in Sarawak. The improved agency coordination despite limited resources, led to the successful arrest and prosecution of six trespassers from Indonesia in April 2018. Financial and time investment in SMART patrols, village anti-poaching patrols, intelligence network and drone technology are vital to achieve higher success yields from ongoing law enforcement efforts at the Landscape.

We recommend the revision and update of action plans and policies to address land-use planning and infrastructure development within key areas for biodiversity. Livelihood development of resident communities and gaining popular support from the urban public should be scaled up. The resident communities provide the first layer of protection as eyes and ears of the enforcement authorities at non-protected sites with orangutans. Meanwhile, the urban public provide the necessary support to influence policy makers in tabling responsible and sustainable Government policies on the environment.



	Gazetted areas	Areas proposed for protection
1. Core habitats	1.1. Lanjak-Entimau Wildlife Sanctuary (LEWS)	1.3. Proposed BANP extensions
	1.2. Batang Ai National Park (BANP)	1.4. Ulu Sungai Menyang Conservation Area
		1.5. Proposed LEWS extension
		1.6. Ta Ann Group's Ulu Pasin Concession Area
2. Remnant sites	2.1. Sedilu National Park	2.4. Proposed Ulu Sebuyau-Sedilu connector
	2.2. Ulu Sebuyau National Park	2.5. Proposed Ulu Sebuyau extension
	2.3. Gunung Lesong National Park	2.6. Proposed Ulu Sebuyau-Gunung Lesong connector
3. Historical ranges	3.1. Bungo Range National Park	3.3. Proposed Klingkang Range National Park
	3.2. Sabal National Park	

Fig. 2.1. Map of sites with conservation interest for orangutans in Sarawak.
Coordinate system: WGS84. This map was created using the software ArcGIS 10.2.1 (www.esri.com) by JP.

Chapter 3.

Population estimates of Bornean orangutans using Bayesian analysis at the greater Batang Ai-Lanjak-Entimau landscape in Sarawak, Malaysia[a]

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3.1. Abstract

The integration of Bayesian analysis into existing great ape survey methods could be used to generate precise and reliable population estimates of Bornean orangutans. We used the Marked Nest Count (MNC) method to count new orangutan nests at seven previously undocumented study sites in Sarawak, Malaysia. Our survey teams marked new nests on the first survey and revisited the plots on two more occasions; after about 21 and 42 days respectively. We used the *N*-mixture models to integrate suitability, abundance and detection models which account for zero inflation and imperfect detection for the analysis. The result was a combined estimate of 355 orangutans with the 95% highest density interval (HDI) of 135 to 602 individuals. We visually inspected the posterior distributions of our parameters and compared precisions between study sites. We subsequently assess the strength or reliability of the generated estimates using identifiability tests. Only three out of the seven estimates had <35% overlap to indicate strong reliability. We discussed the limitations and advantages of our study design and made recommendations to improve the sampling scheme. Over the course of this research, two of the study sites were gazetted as extensions to the Lanjak-Entimau Wildlife Sanctuary for orangutan conservation.

Keywords: Bayesian analysis, Bornean orangutans, Marked Nest Count, plot count, population estimates, *N*-mixture models, Sarawak

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Statement of Authorship

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3.2. Introduction

The world's three orangutan species, Sumatran (*Pongo abelii*), Bornean (*Pongo pygmaeus*) and Tapanuli orangutans (*Pongo tapanuliensis*) are listed as Critically Endangered under the IUCN Red List of Threatened Species, with the latter described and listed in 2017 [1-3]. Threats to orangutan survival have intensified in the past 60 years due to rapid deforestation [4,5], land use conversion into monoculture plantations [6,7], habitat fragmentation [8], illegal wildlife trade and hunting of the species [9,10]. The Bornean orangutan populations suffered more than 25% decline between 1997 and 2015 [11,12] despite an increase in scientific interest and public support. The decline is likely to continue in the immediate future considering social and economic circumstances [13] and the economic importance of oil palm plantations in Malaysia and Indonesia [14].

Due to limited data collection, continued monitoring of orangutan abundance is crucial to assess their population status and rates of population decline [12,15]. This is in line with implementing the Orangutan Population and Habitat Viability Assessment (PHVA) mitigation measures with the goals of maintaining high forest cover at orangutan habitats and improving connectivity between forest patches with orangutans [11,12]. However, it is rarely feasible to acquire accurate population and density estimates from direct counts of orangutans in the wild. The great apes are elusive, solitary and live in small population sizes which require greater effort to detect [13,16].

Researchers in general opted for indirect sign counts to generate population estimates due to constraints on direct counts [16,17]. For orangutans, this means counting nests instead of individuals or groups. The advantages of using nest counts include: a) nests are proxies for orangutans; b) indicator of active habitat use as weaned individuals build nests on an almost daily basis to sleep at night or sometimes to rest during the day; c) higher encounter rates than encounters with great apes; and d) easier measurement of perpendicular distances as nests are stationary [16,17].

Currently, the standard survey protocol to estimate orangutan density consists of: a) counting all nests visible from a line transect or plot; b) generating nest density within the area surveyed; and c) converting nest density into orangutan density using an algorithm [16,18]. There are two methods to generate orangutan density using various parameters: 1) the standing crop nest count (SCNC) method uses nest decay rate, nest construction rate and the records of all nests encountered; and 2) the marked nest count (MNC) method uses only nest construction rate and the records of new nests built within a known inter-survey period [16,18-20].

Both the SCNC and MNC methods are being used for long-term nest monitoring in Borneo and Sumatra [18,21,22]. Although, these methods have limitations, Marshall & Meijaard [23] warned that the nest decay rate in SCNC is the most problematic source of error when used to estimate orangutan density. It is often based on nest decay rates from other sites and time periods when an empirical rate is not available for a particular study region. This approach adds much uncertainty and error to the population estimation because nest decay rates are affected by environmental and biophysical conditions, which vary across space and time [16,24-26].

To bypass nest decay rate, the MNC method uses records of only newly-built nests between the first and the last survey [19,20]. MNC assumes that all new nests were marked and recorded on the first survey, and no new nests built and decayed between the inter-survey periods.

However, despite bypassing nest decay rate, Spehar et al [18] found that the time and effort to acquire reliable and precise density estimates were reportedly the same as the SCNC method. Due to low number of new nests found, past MNC studies of great apes by Plumptre et al [20] and Spehar et al [18] recommended a sample size of 50 new nests and survey effort of more than 200 km of line transects to be sufficient. Thus, the general applicability of this method is limited.

Distance sampling is the most widely used technique to analyse line transect data at present [16,27]. The technique uses detection functions to model the probability of nest detection given the perpendicular distance (or shortest distance) between the observer and the nest. It is expected that the probability of nest detection rapidly decreases with increasing distance from the observer. Nest density estimate is subsequently generated by combining the model with nest encounter rate at the study site. However, the minimum sample size of 60 nests applies to acquire a precise estimate [27]. It is possible to pool nest data from all months to obtain an overall orangutan density estimate for study site with low nest detections [18]. But this may result in imprecise estimates with wide confidence intervals.

In this chapter, we show how the integration of the Bayesian framework into the analysis of density estimates is a novel approach. We applied the *N*-mixture models to simultaneously model suitability, abundance and detection [28]. For the surveys, we opted to use the MNC method and plot survey, instead of the standard line transect (Supplementary Table S3.1). The suitability model relates to whether or not a plot has old or new orangutan nest, which is an indicator of active habitat use; whilst the abundance model refers to new nests abundance given the suitability model. We were able to quantify and visually inspect the most credible range of possibilities and covered 95% of the probability distribution as the highest density interval (HDI) [29]. Finally, we ran identifiability tests to assess the strength or reliability of our estimates [30].

Given the above, the aims of this chapter are to: a) integrate the Bayesian analysis into the MNC method to generate density and population estimates; and b) assess the strength or reliability of these estimates. We conducted nest count surveys of Bornean orangutans (subspecies *Pongo pygmaeus pygmaeus*) at seven previously undocumented study sites in the Malaysian state of Sarawak. We also compared the results with a non-Bayesian approach, discussed the limitation and advantages of using the Bayesian analysis, and the conservation implications of our findings.

3.3. Results

3.3.1. Population and density estimates of orangutans at the study sites

The combined estimate of orangutan population ($\hat{\mu}$) at the seven study sites was 355 individuals with 135 to 602 individuals within the 95% highest density interval (HDI). The combined orangutan density ($\hat{d}$) was 0.5249 individuals km^{-2} with 0.1964 to 0.8842 individuals km^{-2} 95% HDI (Table 3.1 and Fig. 3.1).

Precision and reliability of the estimates

The precision of an estimate is visually inspected by the shape of the histogram. For our study sites, the population estimate at Ulu Katibas had the highest precision. This is visible as the distribution with the narrowest 95% HDI, and the highest and sharpest peak of the seven sites (Fig. 3.1). The distribution at Ulu Sungai Menyang shows that the estimate was less precise with wider 95% HDI and flatter peak than Ulu Katibas, even though it had the highest mean of 115 orangutans. The shape for Ulu Ngemah is notably skewed to the right with the highest peak (mode or the most probably value) at zero. This is the only study site where we were not able to generate an estimate based on the data we collected.

Gimenez et al [30] suggested an identifiability test to assess the strength of an estimate with a guideline that 35% overlap or more between the posterior and prior distributions was 'an indicator of weak identifiability of a parameter'. Out of the seven study sites, the posterior distributions for Batang Ai, Ulu Engkari, Ulu Pasin and Ulu Ngemah had an overlap of more than 35%, which indicated that our orangutan population estimates ($\hat{\mu}$) for these sites were weak. In contrast, the posterior distributions for Ulu Katibas, Ulu Sungai Menyang and Engkari-Telaus were clearly different with overlaps of 22%, 26% and 20% respectively. Thus, our estimates of $\hat{\mu}$ at these sites were strongly reliable and estimable (Fig. 3.1).

Results from a non-Bayesian approach for our datasets show that two of the seven sites had problematic estimates due to low number of new nests detected (Supplementary Fig. S3.1 to S3.3). The combined point estimate using this approach was 313 orangutans with 177-472 as 95% confidence interval. The problematic estimates generated via the bootstrapping analysis were: a) 7 individuals with 95% confidence interval (CI) of 0 to 17 individuals for Ulu Katibas; and b) 37 individuals with 95% CI of 0 to 85 individuals for Engkari-Telaus. The lower limit of 95% CI for a) and b) should include at least one orangutan given new nests were recorded during the inter-survey period. The inclusion of zero orangutan at the lower limit was due to a large proportion of zero values computed from the bootstrapping analysis [31].

<u>Other parameters of interest</u>

A total of 29 plots were surveyed with a combined plot area size of 4.27 km^2 or 0.63% of the combined study area (680.21 km^2) (Supplementary Table S3.2, and Supplementary Fig. S3.4 and S3.5). The average plot size for the 29 plots surveyed was 0.1471 km^2, or four 1-km strips per plot with strip width of 36 m (Supplementary Fig. S3.6 and S3.7). There were 20 plots revisited on the second and third surveys with an average of 42.7 days between the first and the third survey. Two plots were visited on the second survey but not revisited on the third due to logistics constraint. Seven plots were not revisited on the second and third surveys as no old or new orangutan nest detected in these plots on the first survey. Despite the varying survey duration, the information from each plot (t_i, days) were included in the analyses to generate our estimates and measure of reliability.

We used detection of old or new orangutan nest on the first survey ($\hat{\psi}$) as an indicator of habitat use by orangutans at the plots. There were four left skewed distributions for $\hat{\psi}$ with the highest peaks at 1 (Fig. 3.1). Given our data, this was an indication of 100% habitat use by the orangutans present at all plots in Batang Ai, Ulu Engkari, Ulu Pasin and Ulu Sungai Menyang during the survey duration. The highest mean for $\hat{\psi}$ at 87.5% in Ulu Sungai Menyang landscape shows the importance of this non-protected landscape for long-term orangutan conservation. In contrast, the distribution at Ulu Ngemah was right skewed and had the highest peak at zero. But we did not assume habitat use was 0% at the plots since the result in Ulu Ngemah was unestimable given our data during the survey duration. For Ulu Katibas and Engkari-Telaus, not all plots were used by orangutans at the two study sites as shown by the 95% HDI spread around values less than 1 for $\hat{\psi}$ distributions.

There were 40 new orangutan nests recorded by the two teams combined during the first surveys (x) at 29 plots; whilst the total number of new nests recorded on the second and third surveys (y) was 93 new nests (Supplementary Table S3.2). We assessed the estimated probability of detecting new nest by two teams on the first survey ($\hat{q}$).Team 1 missed five nests in total but were recorded by Team 2 from the opposite direction. The estimate of $\hat{q}$ for all the study sites was 0.8133 within 95% HDI of 0.6586 to 0.9412 (Table 3.1). This estimate was used for the detection of new nests in subsequent visits (second and third surveys). As 1.0000 was not within the 95% HDI, not all new orangutan nests were detected even if they were present at the plots.

Given the data, it was also possible to estimate the overall new orangutan nests built during the first surveys at the seven study sites ($\hat{x}_0$). Although 40 new orangutan nests were recorded, the estimate of $\hat{x}_0$ was 43 new orangutan nests within 95% HDI of 36 to 52 nests during the first surveys (Table 3.1). For further information on the data collected and additional results, refer to the Supplementary Appendix S3.1.

3.4. Discussion

Our results show that integrating the Bayesian analysis into the MNC method allowed us to generate more precise estimates even with low counts of new nest. However, we were only able to generate reliable estimates for three of the seven study sites due to insufficient number of plots surveyed in the other four. We acknowledge that time and survey effort invested in the MNC method of this paper was likely the same as the SCNC method from previous studies in Borneo by Spehar et al [18] and van Schaik et al [21]. But we compensate this by quantifying and visually inspecting the precision for all our parameters of interest, in contrast with the uncertainty in nest decay estimation using the SCNC method. In this section, we further discuss the two components of the *N*-mixture models, the limitation and advantages of using the Bayesian analysis in the MNC method, as well as the conservation implications of our paper on the study sites.

3.4.1. Zero inflation and imperfect detection in the *N*-mixture models

One of the initial concerns for the MNC method was the low counts of new nest observed, and not meeting the recommended sample size of 50 new nests and survey effort of more than 200 km. We initially ran the bootstrapping analysis for plots without any new nests (or in very small numbers) but had signs of habitat use by orangutans. Some of these results were indeed problematic with population estimates ranging from zero orangutan and did not fit the standard distributions due to high number of bootstrap samples computed containing the value zero. We then compared this non-Bayesian bootstrapping approach with a Bayesian framework that accounts for subjective belief about our study sites. The first step in our *N*-mixture modelling was then to identify the source of zero inflation and use the models to examine the ecological process.

We adapted Martin et al's [31,32] descriptions into our context for the two types of zero values that vary in four ways. The first type is 'true zero' and it refers to: a) zeros due to random local orangutan extinction at suitable habitats; and b) zeros due to strong ecological processes such as unsuitable habitat from disturbances or poor vegetation quality. The second type is 'false zero' and it refers to: c) zeros from temporary absence due to large home ranges; and d) zeros due to imperfect detection by observers due to the detection process and variability of new nests sampled. To account for definitions b) and d), we combined the zero-inflated Poisson to model new nest abundance given a Bernoulli distribution for site suitability based on plots used or not used ($\hat{\psi}$) as the latent process. The number of new nests recorded (y) was then based on a Binomial distribution to account for imperfect detection ($\hat{q}$) as the observation process [33,34].

However, we made no inferences about true zeros due to local extinction at suitable habitats nor about false zeros due to temporary orangutan absences relative to large home ranges. This is of concern in view that we did not observe any new or old orangutan nest at Ulu Ngemah at all three plots, and did not revisit for the second and third surveys. We made the decision based on Assumption #3 of our methodology as we found no evidence that orangutans were present. Thus, the most appropriate inference for Ulu Ngemah is to say we were 95% certain that habitat use by orangutans at the plots surveyed was less than 5%.

To reiterate, estimates generated via the MNC method in this chapter represent only orangutans present at the plots during the survey period, which is an average of 42.7 days between the first and the last survey. The estimates based on our data were site-specific, reflected a snapshot at a given point in time and did not reflect an overall steady population density at the study sites [18]. Wich & van Schaik [35] noted that orangutans do range extensively across habitats and their abundance in certain areas may correlate to wild fruit abundance at the time. The inference of our estimates then were made after deliberating only habitat use by orangutans within surveyed plots, over a short survey period, and with imperfect detection by observers.

3.4.2. Limitation and advantages of using the Bayesian analysis

Having prior credibility is a critical part of Bayes' Rule [29]. But up to this point, we did not have previous knowledge of orangutan numbers at the study sites. Hence, we opted for an uninformative prior (or flat prior) as our prior credibility. This became problematic for Ulu Ngemah as no old or new nest was recorded at the study site. The posterior distribution for $\hat{\mu}$ then spread widely within 95% HDI of 0 to 109 individuals and had 99% overlap with the uninformative prior, which can be misleading. A more sensible approach to estimate parameter of interest when none of the plots had new nests is to use (or borrow) estimates from nearby study sites as informative priors. The strength and reliability assessment can then be used to measure the posterior-prior overlap percentages to justify the results.

There were three assumptions in this study that determined key decisions when conducting our survey methodology. These assumptions were adapted from the standard MNC method and distance sampling theory [16,27]. All three assumptions were violated at some point, and were either resolved during subsequent surveys, quantified for a measure of precision, or amended for future surveys. Violation of these assumptions meant that we detected less new nests which may have led to an underestimation of nest construction rate, orangutan density and population estimates generated in this study.

Assumption #1 states that 'all orangutan nests present at the plot were recorded on the first survey'. This is adapted from one of the critical assumptions underlying the distance sampling theory except that distance sampling uses line or point transects. Our survey design allowed this assumption to be assessed by having two teams searching each strip for new nests on the same day. There were at least five new nests missed by Team 1 but were later detected by Team 2 from the opposite direction. The assessment result indeed showed probability of detecting new nests ($\hat{q}$) to be < 1, which was at 81.33%, 95% HDI of 65.86% to 94.12%. This shows that not all nests present at the plots were recorded by the two teams.

Assumption #2 states that 'no nest will be constructed and then visible as old before the next survey (21 days later)' [16,19,20]. On at least three occasions, unmarked Class C nests were detected by the teams on subsequent surveys. This could mean that nests were built after the first survey and decayed before the second survey, or the nests were missed on the first survey entirely. Another possible situation that violates this assumption was to have new nests built on the first survey but missed by both teams and was still new when it was detected during the subsequent survey. We addressed this possible violation by conducting one-day training on at least five occasions for inexperienced field assistants and researchers on detecting and observing different nests classes. In addition, for future surveys, we may opt for a shorter inter-survey period of 14 to 21 days [20] to avoid nest decaying before the next survey.

Assumption #3 was the most challenging as we assumed that 'plots with no orangutan nests (old/new) at the first survey were assumed not to be used in the next 42 days (one survey duration) by orangutans, and nest construction rate was zero'. The main reason for this assumption was initially as a cost-effective measure. Our study then does not infer whether unused plots were due to local extinction, temporary absence or a non-habitat for orangutans. But we highly recommend the application of our study design as possible follow up studies in the area, albeit with more plots, more revisits and a different set of research questions.

It is a great advantage for the Bayesian framework in our *N*-mixture models to allow even low counts of new nests to generate precise estimates. However, sufficient number of plots and revisits are prerequisites to generate reliable estimates. For our results, the estimate at Ulu Katibas was the most precise and the second most reliable of the seven study sites despite having only two new nests recorded on the second and third surveys. This was due to five plots surveyed in contrast to only three plots at four study sites with weak estimates. Although the *N*-mixture models do accommodate zero counts, Dénes et al [33] cautioned that the analysis would induce errors if estimates were generated at habitats where the species does not occur. Therefore, previous knowledge of orangutan habitats is also crucial to ensure a precise and reliable estimate at the study site with low or zero counts of new nest.

We believe there is potential to expand the use of MNC and the Bayesian analysis into existing, alternative and/or integrative methods to study great ape population sizes. It is also possible to adapt this method to account for indices of animal density based on sign density such as dung piles or tracks. The end goal of using the MNC method is not just to acquire current density and population estimates given that the method is appropriate for short term studies. But there is also potential to integrate with spatial data to map long term great ape movement, population viability, and seasonal habitat use within a study site [14,18]. Santika et al [11] already applied the Bayesian analysis in an integrated analysis to estimate the rate and drivers of orangutan decline in Borneo. The identifiability tests by Gimenez et al [30] can also take similar analysis a step further by assessing the strength or reliability of the estimates.

3.4.3. Conservation implications on the study sites

The results of this study provided updates on the remaining orangutan populations in Sarawak. This is critical to help develop more effective and proactive conservation strategies for the species. The last reliable estimate of orangutan abundance in Sarawak was published more than two decades ago [36,37], although there have been ad hoc field surveys conducted between 2003 and 2007 [38]. However, the data for the 2003-2007 surveys was not published in a peer-review document as the estimates were deemed inappropriate due to an issue of bias (surveys were conducted only on ridges, following those conducted in 1993 [36]). Nevertheless, internal and donor reports were generated for the surveys conducted at the core orangutan habitats of Batang Ai-Lanjak-Entimau (BALE) landscape. The reports provided an estimate of 1,984 orangutans with 95% CI of 1,175 to 2,582 individuals. However, this estimate is credible only if the whole BALE was homogenous and consisted of ridges.

In 2013, two study sites namely Ulu Katibas and Ulu Pasin were gazetted as extensions to the Lanjak-Entimau Wildlife Sanctuary or LEWS. The data generated from these surveys were instrumental in justifying the creation of the new protected areas. Active habitat use by orangutans at the study sites confirmed their status as high conservation value forests despite the weak estimate at Ulu Pasin and low estimate at Ulu Katibas. The joint partners of this study also proposed a list of prescribed activities including the prohibition of large-scale land use conversion for commercial purposes for the non-protected landscapes of Ulu Sungai Menyang and Engkari-Telaus. This is in line with the Sarawak Government's policy of zero-loss of orangutans and their landscapes since 2016.

3.5. Conclusion

In this chapter, we managed to generate estimates of orangutan density and population even with low counts of new nests. We addressed the concerns of previous studies that required a minimum number of 50 new nests before a precise estimate can be generated. This was resolved by using *N*-mixture models to account for zero-inflation and imperfect detection. The estimated total population for the combined seven previously undocumented study sites was 355 orangutans with 95% HDI of 135 to 602 individuals. However, we found that four out of the seven estimates to be weak and misleading after performing the identifiability tests. The reasons for the weak estimates were due to: a) insufficient plots surveyed at those sites; b) possible violations of the three main assumptions leading to an underestimation of new nests detected; and c) the use of an uninformative prior which became problematic as the posterior distribution had a 99% overlap with its prior distribution, rendering our output not estimable. For future replication of our sampling scheme, we recommend: 1) at least six or more plots surveyed and revisited depending on the simulated outcome of having <35% overlap in an identifiability test; 2) a shorter inter-survey period of 14 to 21 days; and 3) the use of an informative prior with strong reliability from nearby sites to generate more sensible estimates for study sites without old or new orangutan nest detected. The concept for the Bayesian framework and identifiability test of this paper allowed stronger and reliable estimates to be generated with a measure of precision, and it is applicable to existing, alternative and integrative methods for orangutan studies.

3.6. Methods

3.6.1. Study Area

The surveys reported in this chapter were conducted at the greater Batang Ai-Lanjak-Entimau (BALE) landscape in the Malaysian state of Sarawak. The BALE landscape consists of two contiguous protected areas, namely the Batang Ai National Park (BANP) and the Lanjak-Entimau Wildlife Sanctuary (LEWS). The 'greater' BALE landscape refers to the seven sites surrounding the two protected areas that consists of five proposed extension areas (at the time of survey) [39] and two non-protected landscapes (Fig. 3.2). The seven study sites surveyed in chronological order were Batang Ai, Ulu Engkari, Ulu Ngemah, Ulu Katibas, Ulu Pasin, Ulu Sungai Menyang, and Engkari-Telaus. The area sizes of the sites ranged from 22.48 km^2 to 247.80 km^2 and the total area combined was 680.21 km^2 (Table 3.2). For further information on the study sites, refer to the Supplementary Appendix S3.2.

3.6.2. Sampling scheme

In total, there were 42 plots placed at random at the study sites (Supplementary Table S3.1). The purpose of the random placement was to have a better representation of the heterogeneous nature of the greater BALE landscape to include valleys, streams and ridges. Each plot consists of four strips 36 m in width and 1 km in length arranged in a north-south direction (Supplementary Fig. S3.7). At least 3 to 6 experienced people surveyed 18 m from each side of the centre line. The use of 18 m half-width for the plot was derived from previous surveys using Distance sampling at the Batang Ai-Lanjak-Entimau (BALE) landscape between 2003 and 2007 whereby the effective strip half-width was 18 m. For future reference, plot size will apply recommendations by Wich & Boyko of surveying 10 m on either side to reduce the chance of missing nests while walking the centre line.

We surveyed 29 of the plots and had the remaining 13 as reserves (Supplementary Fig. S3.4 and S3.5). For the first five study sites, surveys were conducted at no less than three plots with signs of orangutan nest. If one of the plots had no sign of old or new nest, the reserved plot would be surveyed. But we soon discovered three plots per study site were insufficient and opted to increase the number of plots to six per study site for the latter two study sites. Fieldwork commenced from January 2011 to September 2012, and subsequently continued from October 2013 to May 2015.

The Marked Nest Count (MNC) method [16,19] is a survey technique used in estimating great ape population based on counting and marking new nests built within specific plot (known area size) during a specific time interval (known number of days). New nest is described as with green leaves, and old nest as without green leaf. We used four different nest decay classes adapted from van Schaik et al to refer to nest classification (Supplementary Table S3.5). Old nests were observed at each plot and were later used in the Bayesian analysis to determine the probability of whether orangutans used the plot previously or not.

Nest construction rate ($\hat{D}$) is one of the key features in the MNC. It refers to the density of new nests built between the first and the last survey at plots with known area sizes (nests km^{-2} day^{-1}). To estimate $\hat{D}$, all nests were observed and new nests were marked on the first visit (x). This was to ensure that the latter were not included with the new ones built after the first survey (y). It was assumed that any new nests built after we visited the plot were still visible and were recorded as new 21 days later. The interval between repeat surveys was adequately short to ensure that no new nests constructed between the survey periods can disappear before the next survey [16].

There were three main assumptions used in the survey methodology:

1. All orangutan nests present at the plot were recorded on the first survey.
2. All new nests constructed in the plot after the first surveys were recorded on subsequent surveys.
3. Plots with no orangutan nests (old/new) at the first survey were assumed never to be used or at least were not used in the next 42 days (the survey duration) by orangutan, and nest construction rate was zero.

Additional information on Plot layout, steps for the First survey, followed by Second and Third surveys are found in Supplementary Appendix S3.3.

3.6.3. Bayesian framework for the *N*-mixture models

Kruschke [29] defines Bayesian analysis as the process of reallocating prior credibility consistent with the new data observed. Possibilities that were consistent with the data gain more credibility; possibilities that were not, lose credibility. The Bayesian framework is the structure where the reallocation takes place. All the possibilities were spread out as a probability distribution; thus, the total area under the histogram is equal to 1. The most credible range of possibilities which covers 95% of the posterior distribution is the highest density interval (HDI).

'*N*' refers to abundance. The term 'mixture' in our models is derived from the Binomial/Poisson mixture that we used to estimate abundance of new nests from signs of plot use by orangutans based on the probability of detection by observers [31,33]. We did not use any covariates and opted to use an intercept-only model. We summarize the Bayesian analysis for the *N*-mixture models of this study into three steps (Supplementary Appendix S3.4 and Supplementary Fig. S3.8):

Step 1: Describe the latent and observation processes

1.1. Latent process

1.1.1. Suitability model

Sign of plot use by orangutans (z) is indicated by detection of old or new nest on the first surveys. An indicator variable z_i = 1 was used if signs of old orangutan nest at plot i (i = 1, 2, 3, …, *N*) was available for detection. We had z = 0 for plots without signs of use (this is the zero-inflation part). The relationship for the model depends on a Bernoulli process (z_i, detected or not detected) and varies among plots based on the probability of old nest at a site, ψ. The suitability model given plot use by orangutans is shown in Eq. (3.1):

$$z_i \sim \text{Bernoulli}(\psi_i) \quad \dots \text{ Eq. (3.1)}$$

As a cost-effective measure, plots with z = 0 on the first survey were not revisited.

1.1.2. Abundance of new nests model

The purpose of this model is to find out how many new nests were built between the first and the last visit. The zero-inflated Poisson here captures the latent process of modelling expected new nests abundance (n_i) given spatial variation and the suitability model (z_i). This model is written in Eq. (3.2):

$$n_i \sim \text{Poisson}(\lambda_i \times z_i \times a_i \times t_i), \text{ for } z_i = 1 \quad \dots \text{ Eq. (3.2)}$$

Here, λ is the expected estimate of nest construction rate (nests km^{-2} day^{-1}). We included plot size a (km^2), and the time between the first and last survey t (days) for plots i to get number of nests without the rate units. The λ here refers to the expected nest construction rate if the whole study site was used by orangutans (Supplementary Table S3.3 and Fig. S3.1). This rate is different from the estimated $\hat{D}$ which accounts for plots used and not used by orangutans.

1.2. Observation process

1.2.1. Detection model

This model is based on a Binomial argument that assumes detection probability (q) is independent and identical for all expected abundance of new nests (n_i) at plots i. This relationship is modelled in Eq. (3.3):

$$y_i \sim \text{Binomial}\ (q,\ n_i) \ldots \text{Eq. (3.3)}$$

where q is the probability of detecting new nest by two teams on the first survey. Only the total number of new nests recorded on the second and third surveys (y) is used in this model. The observation y will always be lower than the latent n due to imperfect detection. The number of new nests recorded on the first survey (x) was used to estimate imperfect detection q, as part of assessing Assumption #1. The relationship between x and q is further shown in Supplementary Table S3.4.

Step 2: Generate estimates of nest construction rate, orangutan density and population

2.1. Estimate of nest construction rate

We weighted the expected estimate of nest construction rate ($\hat{\lambda}$) with the probability of old nest at a site ($\hat{\psi}$) so as not to lose information about habitat use by orangutans. We show the estimated nest construction rate ($\hat{D}$) for the whole study site, used and not used by orangutans in Eq. (3.4):

$$\hat{D}_M = \hat{\lambda}_M \times \hat{\psi}_M \ \ldots \text{Eq. (3.4)}$$

where *M* is the study site in chronological order: Batang Ai, Ulu Engkari, … Engkari-Telaus (M = 1, 2, … 7).

2.2. Estimates of orangutan density and population

After generating the estimated nest construction rate, we determine the estimated orangutan density, $\hat{d}$ (orangutan km^{-2}) at the study site using Eq. (3.5):

$$\hat{d}_M = \frac{\hat{D}_M}{\hat{p} \times \hat{r}} \ \ldots \text{Eq. (3.5)}$$

where, $\hat{p}$ = estimated proportion of nest builders in the population

$\hat{r}$ = estimated daily rate at which nest-builders build nests (nests orangutan^{-1} day^{-1})

$\hat{p} \times \hat{r}$ = number of nests built per orangutan per day

Orangutan follows to determine $\hat{p} \times \hat{r}$ for the BALE landscape was unsuccessful in past attempts which were conducted from September to November 2006 [38]. Instead, we used the results by Ancrenaz et al [22] for the values of $\hat{p} \approx 0.85$ (given n = 92 individuals) and $\hat{r} \approx 1.00$ (given 602 dawn-to-dusk follows) obtained at Kinabatangan, Sabah.

We then determine the estimated orangutan population at each study site throughout the duration of the survey ($\hat{\mu}$) using Eq. (3.6):

$$\text{Estimated orangutan population, } \hat{\mu}_M = \hat{d}_M \times \text{Total area size of each study site}_M\ (\text{km}^2) \quad \text{... Eq. (3.6)}$$

Step 3: Assess strength or reliability of the estimates

3.1. Identifiability test

This test by Gimenez et al [30] is a simple guideline to check the identifiability of any parameter of interest (θ) by declaring it weak for overlap of >35% between the marginal prior and its marginal posterior distributions. The percentage overlap (τ_θ) between the two distributions for data Y is shown in Eq. (3.7):

$$\tau_\theta = \int \min(p(\theta), \pi(\theta \mid Y))\,\mathrm{d}\theta \quad \text{... Eq. (3.7)}$$

where $p(\theta)$ is the marginal prior distribution, and $\pi(\theta|Y)$ is the marginal posterior distribution. The estimates for the parameter θ is said to be weak and misleading when $\pi(\theta|Y) \approx p(\theta)$.

3.6.4. Implementation in programme R

We used the Markov chain Monte Carlo (MCMC) [40] to perform the Bayesian analysis for our *N*-mixture models and to estimate uncertainty for better interpretation of the results. We ran the estimation in Just another Gibbs sampler or JAGS [40] using the `R2jags` interface [41] in programme R (version 3.4.3) [42]. We used the `coda` package developed by Plummer et al [43] and `R2jags` package version 0.5-7 developed by Su & Yajima [41] to run the models.

We used uninformative priors: a uniform [0,1] prior for $\hat{\psi}$, and a uniform [0,4] prior for $\hat{\lambda}$. Prior sensitivity analysis showed that the latter was uninformative. The analysis converged quickly, and 40,000 iterations were used, of which 5,000 were discarded as burn-in. The mean and 95% highest density interval (HDI) of the MCMC samples were used to summarise the posterior probabilities.

In order to assess the strength and reliability of the generated estimates, the posterior and prior distributions were made to overlap using the function `postPriorOverlap` within the `wiqid` package version 0.1.3 developed by Meredith [44]. The complete R scripts for these analyses are shown in Supplementary Appendix S3.5.

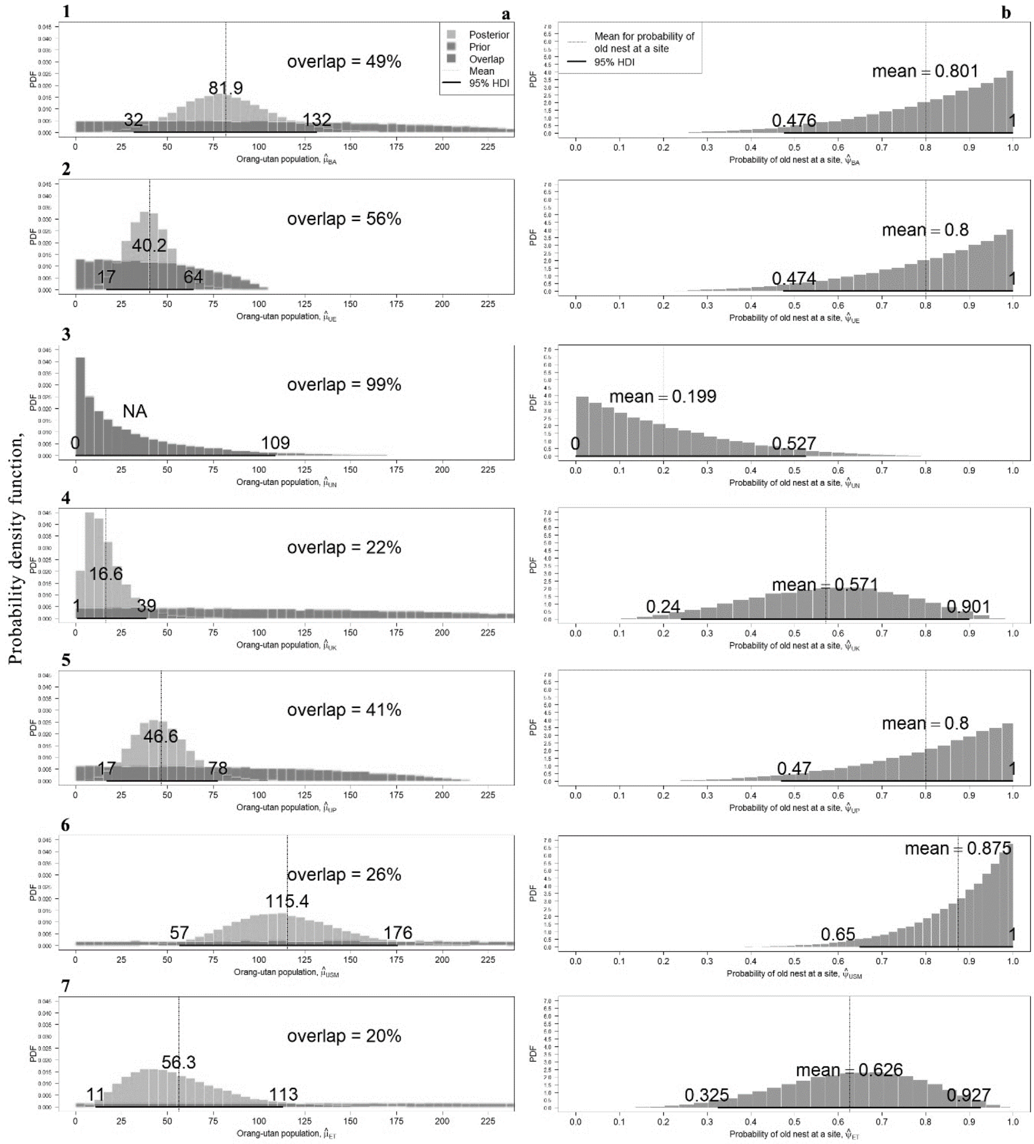

Fig. 3.1. The probability density function of: a) prior and posterior estimates of orangutan population, and b) probability of old nest at a site with 95% HDI at the seven study sites. The row sequence corresponds to the study sites: 1) Batang Ai, 2) Ulu Engkari, 3) Ulu Ngemah, 4) Ulu Katibas, 5) Ulu Pasin, 6) Ulu Sungai Menyang, and 7) Engkari-Telaus.

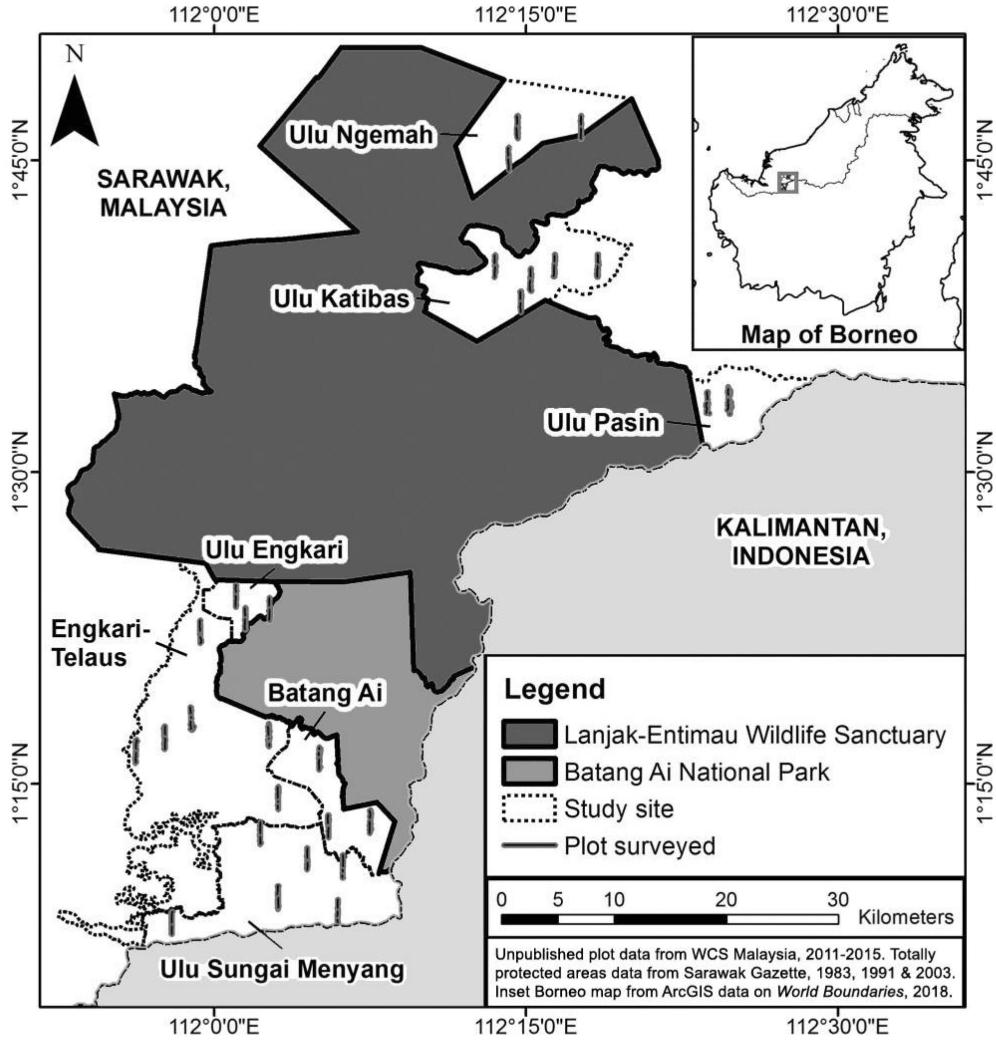

Fig. 3.2. Map showing the study sites located adjacent to the two main protected areas (Lanjak-Entimau Wildlife Sanctuary and Batang Ai National Park), and the locations of plots surveyed throughout the survey duration from 2011 to 2015.
This map was created using the software ArcGIS 10.2.1 (www.esri.com) by SN and JP.

Table 3.1. Estimates of probability of detecting new nest ($\hat{q}$), new orangutan nests recorded on the first survey ($\hat{x}_0$), orangutan density, $\hat{d}$ (orangutans km^{-2}), and orangutan population ($\hat{\mu}$) with 95% HDI for the study sites.
We do not have an estimate of orangutan population at Ulu Ngemah given that there was no evidence of habitat use by orangutans during the survey duration. We assigned 'NA' for the estimates.

Study site	Acronym	$\hat{q}$ (95% HDI)	$\hat{x}_0$ (95% HDI)	Estimate of orangutan density			Estimate of orangutan population		
				$\hat{d}$	Lower HDI	Upper HDI	$\hat{\mu}$	Lower HDI	Upper HDI
1. Southern (Batang Ai)	BA	0.8133 (0.6586 to 0.9412)	43.4237 (36.0003 to 52.6110)	1.4050	0.5440	2.2586	**82**	**32**	**132**
2. Northern (Ulu Engkari)	UE			1.7890	0.7442	2.8663	**40**	**17**	**64**
3. Ulu Ngemah	UN			0.4681	0.0000	1.5696	**NA**	**NA**	**NA**
4. Ulu Katibas	UK			0.1719	0.0080	0.4014	**16**	**1**	**39**
5. Ulu Pasin	UP			1.0174	0.3682	1.6944	**46**	**17**	**78**
6. Ulu Sungai Menyang	USM			0.8245	0.4052	1.2554	**115**	**57**	**176**
7. Engkari Telaus	ET			0.2273	0.0434	0.4571	**56**	**11**	**113**
Total combined estimate with 95% HDI at the study sites:				**0.5249***	**0.1964***	**0.8842***	**355**	**135**	**602**

*Note: The density estimates here were weighted by the area size of the study sites.

Table 3.2. The study sites referred to in Chapter 3 and their area sizes.
The protection status of each study site (proposed, gazetted as extension, or non-protected) is also indicated. The acronym BANP refers to Batang Ai National Park, and LEWS refers to Lanjak-Entimau Wildlife Sanctuary.

Study site	Acronym	Protection status	Size (km^2)
1. Batang Ai	BA	Proposed Southern extension of BANP	58.28
2. Ulu Engkari	UE	Proposed Northern extension of BANP	22.48
3. Ulu Ngemah	UN	Proposed extension of LEWS	69.40
4. Ulu Katibas	UK	Extension of LEWS (proposed at the commencement of surveys, became part of the sanctuary in 2013)	96.41
5. Ulu Pasin	UP	Extension of LEWS (proposed at the commencement of surveys, became part of the sanctuary in 2013)	45.84
6. Ulu Sungai Menyang	USM	Non-protected landscape	140.00
7. Engkari-Telaus	ET	Non-protected Community Conservation Landscape	247.80
		Total area size=	**680.21**

Chapter 4.

Occupancy modelling of orangutan distribution at the greater Batang Ai-Lanjak-Entimau landscape in Sarawak, Malaysia[a]

Joshua Pandong[b,c], Melvin Gumal[b] and Lian Pin Koh[c,d]

4.1. Abstract

The knowledge on orangutan distribution is currently imperfect and investigation of into methods such as the occupancy modelling could be used to map orangutan occurrence over time and space. This is by way of using survey records of new orangutan nests as proxies to indicate great ape distribution during the survey period. We spatially indexed 354 hexagonal tiles as sampling units over the Batang Ai-Lanjak-Entimau landscape. Using a Bayesian framework, we predicted occupancy probability at a tile given occupancy of new nests in its neighbouring tiles, with a measure of imperfect detection. We determined the occupancy probabilities of new orangutan nests recorded over a sampling season, that is 42 days between the first and third survey. The 42-day duration was regarded as a 'simultaneous event' at the landscape as part of an academic exercise. The results show higher occupancy probabilities to the south of the landscape, a result similar to what was shown from surveys in the 1990s. Tiles with higher degree of variability or uncertainty were at plots with no old or new orangutan nest recorded during the surveys. We fine-tuned the study design for potential re-surveys at the landscape and future surveys at other sites with remnant orangutan populations. We also recommended tiles with high occupancy probabilities as priority sites for conservation and enforcement.

Keywords: Bornean orangutans, detection probability, distribution map, hexagonal tiles, nest count, spatial autologistic.

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Statement of Authorship

Title of Paper	Occupancy modelling of orang-utan distribution at the greater Batang Ai-Lanjak-Entimau landscape in Sarawak, Malaysia
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Name of Principal Author (Candidate)	Joshua Juan Anak George Pandong (to appear as Joshua Pandong)		
Contribution to the Paper	I wrote 80% of the manuscript, refined the study design and methodology, performed the analysis, and created the maps.		
Overall percentage (%)	80%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	13 September 2018

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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4.2. Introduction

The orangutans (*Pongo* spp) are the only great ape in Asia and found on the islands of Sumatra and Borneo [1,2]. The three species are namely the Sumatran (*P. abelii*), Bornean (*P. pygmaeus*) and Tapanuli orangutans (*P. tapanuliensis*) [3-5]. The three orangutan species are listed as Critically Endangered under the IUCN Red List of Threatened Species. In the past 60 years, threats to orangutan viability and conservation have escalated at an alarming level. Sumatra lost approximately 60% of its key orangutan forest habitat (11,570 km^2) between 1985 and 2007 [6]. Borneo lost approximately 24% (70,000 km^2) of core orangutan range between the 1950s and 2010 [7]. The drastic decline of orangutan habitats can be attributed to several causes, mainly forest conversion into plantations, hunting, encroachment, fire, and shrinking fragmented habitats [8-11].

Continued monitoring of orangutan population and distribution across various land use types have been crucial to assist researchers and managers in making informed decisions on conservation and enforcement [12,13]. In Borneo, this is important as 24% of orangutan distribution occurs outside of protected areas (36,542 km^2) and a further 49% in concessions expected to be converted to plantations (74,373 km^2) [11]. These mixed landscapes include oil palm plantations used by orangutans to move between forest patches [14], and communal lands without legal protection status but are viable habitats for orangutans [11]. As part of the continued monitoring effort, researchers incorporated various sampling techniques and technology to map prediction of orangutan distribution across various habitat units and land use types [7,13,15,16].

One key factor that naturally affect orangutan distribution is food availability. Orangutans respond to seasonal fruit availability by changing their ranging strategy and diet composition [17,18]. Buij et al [19] recorded higher nest counts and biased use of home ranges at Ketambe study site during periods of high-fruit abundance compared to the annual average for the wider Ketambe region. In addition, orangutans are also known to range up to 25 km^2 to maintain an adequate diet [20]. To prevent bias in population estimate, Husson et al [15] applied a standardization process to control the effects of this difference to reflect a 'real' or stable population estimate throughout the year. However, they also cautioned that the nest decay rate from other sites and different time periods is the largest source of potential error when used to estimate orangutan population [21-24], but extrapolations of such rates are still commonly found in current orangutan conservation studies.

To improve existing techniques, a basic occupancy study design could be used to assess spatial distributions of wide-ranging and elusive species [25,26] without the complexities of a standardization process or the use of problematic covariates such as nest decay rate. This involves surveying several sampling units or habitat patches within the larger study area to record signs of species presence or to determine resource use by the target species [25,27]. Each sampling unit is visited by one or more trained observers to detect animal signs and in more than one visit to help account for false negatives. The modelling approach then deals with imperfect detection of animal signs at neighbouring sampling units [26], which are subsequently used for prediction and inference of species occupancy at the given sampling unit over the larger landscape.

For this study, we used unpublished data provided by the Wildlife Conservation Society (WCS) Malaysia to produce a brief snapshot of orangutan presence at the core habitats of the Batang Ai-Lanjak-Entimau (BALE) landscape. The surveys were initially conducted to generate population estimates of orangutans at the landscape [28]. However, the authors found that despite being identified as suitable habitat, portions of the BALE landscape were without signs of old or new orangutan nest. The cause of this observation may be due to random local extinction or temporary absence. Our study design could then be used to form the basis for future surveys to examine and where possible, determine causes for these non-detections. In this study, we sought to examine spatial distribution of orangutans at the landscape at a given point in time.

The data covered two survey periods: 2003 to 2007 and 2011 to 2015. Despite the different sampling schemes, both surveys had data on new orangutan nests built between three visits, that is 42 days between the first and the third visit. We made the simplifying assumption that the surveys were a 'simultaneous event' as part of an academic exercise to simplify reality for the development of this study design. All transects and plots were treated as surveyed within the same 42 days. We therefore bypass the use of nest decay rate as we only used records of new orangutan nests built within the 42-day window [21,29]. We also used the new nests data as an indicator of orangutan foraging strategy [19] due to the lack of fruit production data at the study area.

We applied a spatial autologistic model on a tessellation of hexagonal tiles to analyse data sampled from various areas within the BALE landscape [25,26]. We used Singleton & van Schaik's [20] minimum home range size of an adult female orangutan as the area size of each tile, that is 8.5 km^2 per tile. The model uses occupancy with imperfect detection of new nests in neighbouring tiles to predict the occupancy probability at the given tile with a measure of precision (coefficient of variation or CV) [30,31]. The advantages of using hexagonal tiles over common square grids include: a) suitable connectivity for orthogonal movements; b) equal length sides and identical nearest neighbours; c) lowest perimeter to area ratio (after a circle) to form a grid; and d) better fit for curved surfaces [32,33]. We also adopted a Bayesian framework and used Markov chain Monte Carlo (MCMC) for inference [25,34].

Given the above, the aims of this academic exercise were to: a) determine the occupancy probability of orangutans (subspecies *Pongo pygmaeus pygmaeus*) using records of new nests across the BALE landscape, b) assess the degree of variability or uncertainty of the results, and c) generate proxy orangutan distribution maps for conservation planning. We further discussed improvements of the study design for future surveys, limitation and advantages of using the occupancy modelling, and the conservation implications of our findings.

4.3. Results

The map of observed occupancy (Fig. 4.1) shows that there were 70 out of 354 hexagonal tiles (each tile was 8.5 km^2 in size) where new orangutan nests were recorded (y = 1). We surveyed 38 tiles without recording any new orangutan nest (y = 0) and did not survey 245 tiles. For this academic exercise, we assumed that the surveyed tiles followed the marked nest count (MNC) method [29,35], which meant repeat surveys were conducted in three visits within a 42-day survey period between the first and the last survey.

Given our data, 100 out of 354 tiles were with high occupancy probabilities (ψ > 0.60). These were mainly at the central and southern portions of the greater BALE landscape (Fig. 4.2). The seven tiles with ψ > 0.76 were concentrated at the Batang Ai National Park (BANP) and the Ulu Sungai Menyang Conservation Area. This supports previous findings that the highest orangutan population density is located there [36]. There were 62 tiles with occupancy probabilities of < 0.27. These were mainly located at the western and northern portions of the greater BALE landscape where surveys yielded no new orangutan nest.

The posterior coefficient of variation (CV) map (Fig. 4.3) fits well when visually compared to the observed occupancy map (Fig. 4.1). This means the degree of variability or uncertainty becomes higher for tiles without detection of new orangutan nest or at unsurveyed tiles that were spatially far from the surveyed tiles. Thus, we used the posterior CV as an indicator of how strong (lower CV) or weak (higher CV) the point estimate was for each tile [25].

Two other notable results generated were probability of detection and spatial autologistic parameters. Probability of detection (p) was at 0.9955 with 0.9640 to 1.0000 within the 95% highest density interval (HDI). However, this is unreasonably high and would have meant that teams conducting surveys detected new orangutan nests 99.55% of the times the nests were present. The probability of non-detection (for three visits) would then be too low for practical purposes, especially for unsurveyed tiles. For the spatial autologistic parameters, the intercept alpha was -2.5 and the coefficient beta was 5.0. This verifies that tiles were less likely to be occupied if the number of occupied neighbours were zero, and vice versa.

4.4. Discussion

Our results show that the occupancy modelling allowed us to use new orangutan nests as proxies to map orangutan distribution across surveyed tiles and their neighbouring unsurveyed tiles for the period of the surveys. However, the glaring issues of unreasonably high probability of detection as well as the high variability or uncertainty in the posterior CV show that much adjustments are needed to fine-tune the sampling scheme. In this section, we discuss ways to improve the study design for an occupancy analysis, the limitation and advantages of using the occupancy modelling, as well as the conservation implications of our paper for orangutan conservation and management.

4.4.1. Study design improvements

4.4.1.1. Probability of detection

The unreasonably high probability of detection for our data was due to the non-independent observations by two teams during the repeat surveys. The sampling scheme followed the MNC method; all new nests detected by Team 1 were marked, and Team 2 only recorded any new nests missed by Team 1 from the opposite direction. Team 2 would have then spotted nests marked by Team 1 en route but did not record them, hence the non-independence [28]. This assessment was useful to account for probability of detecting new nests by two teams. However, for our study, probability of detection at the hexagonal tiles (p) was estimated based on the three survey occasions, not the two teams. Therefore, high p was expected given detections were high during each survey, if new nests were present.

There are other ways to obtain an unbiased species occupancy using replication at sampled sites to address imperfect detection [37]. In our study, multiple surveys within a sampling season is not the only method to assess probability of new nest detection [34]. Two options to be considered are deploying multiple independent observers or surveying multiple sub-tiles within a sampling unit. Each option deserves careful attention prior to implementation. The first option may require multiple observers to conduct independent surveys, either on the same or different visit [27]. The second option requires a higher resolution tessellation which would comprise of groups of seven hexagonal sub-tiles per sampling unit also known as the General Balanced Ternary [33] and uses a spatial hierarchical model for analysis [32].

A third option to assess the probability of detection is to increase the number of repeat surveys to be more than three. At present, the low probability of false negatives in our study shows that more sampling units are needed to be surveyed rather than increase number of surveys per sampling unit [27]. The third option is then implemented only if the detection probabilities start to decrease as more sampling units are surveyed. Again, we caution that decisions should be based on project objectives. Mackenzie [34] recommends shorter survey or minimal sampling periods in a season. If a sampling season is too long, orangutans may appear present in all or appear to use all sampling units within the study area. But if it is too short, a sampling season may not provide sufficient opportunity for researchers to encounter new nests.

4.4.1.2. Coefficient of variation (CV)

The high variability or uncertainty in the posterior CV was due to the high number of unsurveyed tiles that were spatially far from the surveyed tiles as well as tiles without detection of new orangutan nest included in the analysis. Currently, there is a lack of surveys in the centre region between the two zones with high concentration of occupancy probability ($\psi > 0.60$). The posterior CV map provides a visual guide for researchers and conservation practitioners at the landscape to plan future surveys at tiles with $\psi < 0.60$ and CV > 0.23, if an investigation is needed. Otherwise, more tiles selected at random with replacement could be surveyed as part of a larger-scale occupancy surveys and monitoring across the landscape in the future [38].

4.4.2. Limitation and advantages of using the occupancy modelling

The inference about orangutan distribution made using this study design heavily depends on the method used to collect new nest data and the measure of imperfect detection estimated from them. WCS Malaysia initially collected the data in both survey periods to generate population estimates at the BALE landscape using the MNC method over a 42-day sampling season. We subsequently treated the new nest data as occurrence data to draw inference about orangutan distribution in this chapter. However, the differing outcomes of population estimates and species distribution meant that distinct study objectives and different sampling designs were required for the two [27]. Below, we further discuss a potential study as a follow up from the lessons learned via both the population and distribution studies at the BALE landscape.

At present, the immediate objective for future surveys is to gain more understanding on the extent of orangutan distribution across the BALE landscape. There were portions of the BALE landscape without signs of old or new orangutan nests during the surveys conducted between 2003 to 2007 and 2011 to 2015 even though the area was deemed as suitable habitat [39,40]. Occupancy modelling could then be further developed to explore possible reasons for change across time and space. Spatial distribution of orangutans is crucial as population estimates are generated from multiplying habitat area size with orangutan density. However, without a representation of distribution (or lack of) in unoccupied habitats, it leads to an overestimation of population estimate based on suitable but unoccupied habitats.

Optimal number of tiles to be surveyed and the number of repeat surveys per tile must be determined in order to reduce high variability of CV. Mackenzie & Royle [27] suggested that the "optimal strategy for rare species is to conduct fewer surveys at more sites, while for a common species … conduct more surveys at fewer sites." This means survey design for rare species with low occurrence such as orangutans should emphasize surveys at greater number of tiles at the expense of repeat surveys. For future surveys, we concur with Mackenzie & Royle [27] as well as the caveat indicated by Mackenzie [34] to have more tiles selected and surveys done in a shorter timeframe or sampling season. We also intend to continue having random selection of tiles and with replacements, to avoid biasing it to easy-to-access or favoured sites.

Probability of detection would then be estimated by surveying sub-tiles within a sampling unit using the General Balanced Ternary and spatial hierarchical model. In addition, multiple teams should survey adjacent tiles on the same days whenever possible to allow detection under similar conditions across the study area [26]. The change in occupancy probabilities between multiple sampling seasons and across the landscape could infer trends about orangutan movement and possibly about dispersal, colonization at the tiles by orangutans or perhaps temporal or local extinctions at the tiles if orangutans had not been observed in the area for decades.

4.4.3. Conservation implications for orangutan conservation and management

This academic exercise can help assist researchers and managers in learning about occurrence and habitat use of orangutans across the BALE landscape. The map of occupancy probabilities provided a current distribution of orangutans at the landscape. Hexagonal tiles with high occupancy probabilities that were clumped together were an indication of highly used habitats during the sampling season [26]. In our study, we identified 100 out of 354 tiles with ψ > 60% as priority sites with strong orangutan presence. Using this information, researchers and managers can examine the characteristics of the occupied and unoccupied tiles as part of investigating orangutan and habitat associations there.

If integrated into population studies, the BALE landscape could then be stratified to determine different population estimates at various habitats during a sampling season. This is critical for reliable inferences for conservation and enforcement, amid increasing land development around the study area over time. We designed this study to use new nest data only and excluded old nests to provide distribution of orangutans during a sampling season. A different study design using new and old nest data could potentially be developed using this occupancy approach for conservation practitioners collecting both datasets.

4.5. Conclusion

In this chapter, we showed that the occupancy estimation and modelling based on detection–nondetection of new nest data could be used as proxies to map current orangutan distribution across the BALE landscape during the project period. The aim of this academic exercise was to use a tessellation of hexagonal tiles to determine occupancy probability of orangutan across the landscape. However, the unreasonably high probability of detection and variability or uncertainty in the posterior CV show that much adjustments are needed to fine-tune the sampling scheme. We recommend more independent sampling units or tiles conducted in shorter timeframe, as a substitute for repeat surveys, for larger-scale occupancy surveys and monitoring in the future. We believe that occupancy modelling could be further developed as an effective way to explore change in distribution across time and space especially for orangutans as the species is not always detected with certainty. The ideal use of occupancy modelling at the BALE landscape in our opinion is to use it as an integrative approach with population studies. With an integrated approach, it is possible to map the orangutan population and movement across various habitats over multiple short sampling seasons. In this way, we can avoid overestimation of population estimate based on suitable but unoccupied habitats.

4.6. Methods

4.6.1. Study Area

Our study site consists of four contiguous areas with different land statuses: 1) areas with legal protection status, namely the Batang Ai National Park (BANP) and the Lanjak-Entimau Wildlife Sanctuary (LEWS), collectively known as the Batang Ai-Lanjak-Entimau (BALE) landscape; 2) areas gazetted as extensions to LEWS, namely Ulu Katibas and Ulu Pasin; 3) three proposed extension areas to BALE: Batang Ai, Ulu Engkari and Ulu Ngemah; and 4) two non-protected areas of Ulu Sungai Menyang and Engkari-Telaus (Fig. 4.4). The area sizes ranged from 22.48 km^2 to 1,687.60 km^2, and the total area combined was 2,608.21 km^2 (Table 4.1).

4.6.2. Data source

WCS Malaysia conducted orangutan nest count surveys at the study area in two different periods: a) between 2003 and 2007 at the BALE landscape, and b) between 2011 and 2015 at the seven areas outside BALE [28]. The teams used the marked nest count (MNC) method for both surveys. However, the sampling schemes for the nest counts were different: 1) Distance sampling along line transects for the 2003-2007 surveys; and 2) randomly-placed plots for the 2011-2015 surveys. There were up to three visits conducted at each transect or plot, about 42 days between the first and third survey. The 21-day interval was assumed to be sufficiently short before a new nest (with green leaves) becomes old (no green leaf) when detected in subsequent survey.

The length of the transects during the 2003-2007 surveys were 2 km at BANP and 3 km at LEWS, with an effective strip half-width at 18 m based on the analysis using the software Distance 4.3 [41]. The average area size of the plots during the 2011-2015 surveys was about 0.1440 km^2; one plot consists of four 1-km strip each with a strip width of 36 m. The plot size was designed to accommodate travel between two strips per team in one day; and the additional pair of strips allowed for higher new nest detection in one plot, thus reducing travel time between plots to observe similar number of new nests. We used only records of new orangutan nests detected at transects and plots for our analysis to reflect proxy distribution of orangutans only during the survey duration.

The study area was divided into a tessellation of hexagonal tiles based on Johnson et al [25] in ArcMap 10.2.1 (www.esri.com). The hexagonal design allows the tiles to have six identical and evenly spaced neighbouring units, with distance between all neighbours and the centroids to be the same [32,33]. Ideally, the survey routes would have followed the method by Magoun et al [26] where a survey route was plotted through a tile centre, exited another side (with all sides had the potential to be included), and then entered the next tile in the direction of the tile centre. However, we did not perform the ideal method and opted to overlay the tessellation on existing transects and plots for the two survey periods as a post hoc academic exercise.

A total of 354 tile units were overlaid across the landscape with 108 of those tiles ‘surveyed’ (Fig. 4.1). The individual tile size was 8.5 km^2. This corresponds to a minimum female orangutan home range size based on the study by Singleton & van Schaik [20]. We chose this area size as the orangutan follows in this home range study were the most extensive and recent among the published estimates listed in Singleton et al [42]. We subsequently conducted the analysis to acquire a spatial overview of the landscape with a simplifying assumption that all surveys were conducted during the same 42-day window.

4.6.3. Model framework

We used the spatial autologistic model to map occupancy probability of new orangutan nest at each hexagonal tile and accounted for imperfect detection [31]. The occupancy process (ψ) is the primary interest in this analysis. Occupancy probability for tile i (ψ_i) is modelled as a logistic function of the proportion of neighbouring tiles occupied.

The probability of detection (p) allowed us to assess false zeros due to imperfect detection between visits due to the detection process and variability at the tiles sampled. We summarize the Bayesian analysis for the spatial autologistic models of this study into three steps:

Step 1: Identify the number of occupied neighbours

We overlaid a neighbourhood of non-overlapping hexagonal tiles across the study sites. Each tile unit shares boundary with its neighbours, and has between two to six neighbours. We identified x_i, the number of occupied neighbours of tile i (i = 1, 2, 3… G), and modelled this relationship using a model by Royle & Dorazio [31] as a reference shown in Eq. (4.1) below:

$$x_i = \frac{1}{n_i}\left(\sum_{j \in N_i} z_j\right) \quad \text{… Eq. (4.1)}$$

The notation n_i refers to the number of neighbours each tile has. N_i is a matrix of $G \times \max(N_i)$, where: a) G refers to 354 rows of hexagonal tiles, and b) max(N_i) indicates which of tiles j are neighbours to tile i based on n_i in each row. The latent variable z denotes the occupancy status of new orangutan nest at the tile during the surveys.

Step 2: Describe the latent and observation processes

To differentiate between variation in detectability and occupancy, we first introduce the distinction between latent process (underlying state variable observed imperfectly) and observation process [31]. This is denoted by the latent z and observation y. To accommodate imperfect sampling, we recognized that y is equal to z only sometimes, and at other times, we may falsely observe y = 0.

There are two possible mechanism for non-occupancy observations. Firstly, ‘sampling zero’ means new orangutan nest was present but not detected. Second, ‘structural zero’ refers to no new nest was built by some random chance at a suitable habitat [34]. However, we have no way of knowing which of the two occur when y = 0. Thus, probability of detection (p) is the probability of observing new orangutan nest over multiple surveys, given that it is present. Occupancy probability is the probability of tile occupied when z = 1. Details of the relationship between p and ψ are described below:

4.6.3.1. Latent process:

We implied that occupancy status of sites does not change for detection probability and occupancy probability estimation, which is the closure assumption. This meant repeat surveys were not conducted and separated by a long break (up to one year). In our survey design, we assumed that the occupancy states of $z_1, z_2, z_3, \ldots, z_G$ were spatially dependent within the landscape structure. The standard framework for modelling spatial dependence in a binary state variable is the use of the spatial autologistic model. The set of possibilities for the latent z has two values: z = 1 for 'occupied' or z = 0 for 'not-occupied'. For tiles that were not surveyed, we needed to obtain a prediction on how many of the unsurveyed tiles were occupied. The relationship for the model depends on a Bernoulli process (z_i , detected or not detected) and varies among tiles based on the occupancy probability, ψ. The relationship is shown in Eq. (4.2):

$$z_i \sim \text{Bernoulli}(\psi_i) \; \ldots \text{Eq. (4.2)}$$

We specified a functional relationship between ψ and the spatial auto-covariate x_i in a linear relationship form using the logit link function in Eq. (4.3):

$$\text{logit}(\psi_i) = \alpha + \beta x_i \; \ldots \text{Eq. (4.3)}$$

where α and β are parameters to be estimated. We chose the logit link function to model the probability of 'success' occupancy as a function of covariates [34]. The purpose of the logit link is to take a linear combination of covariate values and transform those values to the scale of probability, i.e. between 0 and 1. x_i are expected to be constant over three survey occasions.

4.6.3.2. Observation process:

It is vital that imperfect detection of new orangutan nest be considered to infer about occupancy probability [27]. Ignoring imperfect detection would have understate the occupancy probability and distribution. The observation y refers to the number of occasions on which new orangutan nest was detected at the tile; 'NA' if the tile was not surveyed. This model is based on a Binomial argument that assumes detection probability (p) is independent and identical for all expected parameter $p \times z_i$. Thus, if the tile is occupied (z_i = 1), the observations are binomial with parameter p. Conversely, if the tile is unoccupied (z_i = 0), then observations are binomial with probability 0 (i.e. the observations must be zero). This relationship is modelled in Eq. (4.4):

$$y_i \sim \text{Binomial}(K, p\, z_i) \; \ldots \text{Eq. (4.4)}$$

where K is the total number of occasions at each tile (three survey occasions). However, this is irrelevant if the tile was not surveyed, but it must not be assigned as 'NA' in the analysis.

We could run Steps 1 and 2 using WinBUGS, that is specifications for an autologistic model with observation of the state variable z subject to imperfect detection [31].

Step 3: Assess the variability or uncertainty of the estimates

The coefficient of variation (CV) is a measure of relative variability. It is the ratio of the standard deviation (SD) to the mean. The CV is useful to compare results between tiles that have different measures or values [25]. Thus, the posterior CV is a useful indicator of how 'good' the point estimate for occupancy probability is at each tile. 'Good' here refers to the spread of the posterior around the point estimate. Thus, higher CV means more variability or uncertainty, and vice versa for lower CV. From our results, there were more variability or uncertainty in regions that were spatially far from the surveyed tiles and at tiles with unobserved occupancy or sparse sampling effort. The equation for posterior CV in percentage is shown in Eq. (4.5):

$$\%\text{CV} = \left(\frac{\text{SD}_{\psi}}{\text{Mean}_{\psi}}\right) \times 100\% \ \ldots \ \text{Eq. (4.5)}$$

4.6.4. Bayesian analysis using WinBUGS and implementation in R

Kruschke [43] defines Bayesian analysis as the process of reallocating prior credibility consistent with the new data observed. Possibilities that were consistent with the data gain more credibility; possibilities that were not, lose credibility. The Bayesian framework is the structure where the reallocation takes place. All the possibilities were spread out as a probability distribution; thus, the total area under the histogram is equal to 1. The most credible range of possibilities which covers 95% of the posterior distribution is the highest density interval (HDI).

We adopted a Bayesian perspective and used Markov chain Monte Carlo (MCMC) [44] for inference on the occupancy probabilities and imperfect detection estimates of this study. We ran the occupancy model in WinBUGS [45] using the `R2WinBUGS` interface [46] in R (version 3.4.3) [47]. The analysis converged quickly, and 25,000 iterations were used of which 5,000 were discarded as burn-in. The mean and 95% highest density interval (HDI) of the MCMC samples were used to summarise the posterior probabilities. The complete R scripts for these analyses are shown in the Supplementary Materials (Appendices S4.1 to S4.3).

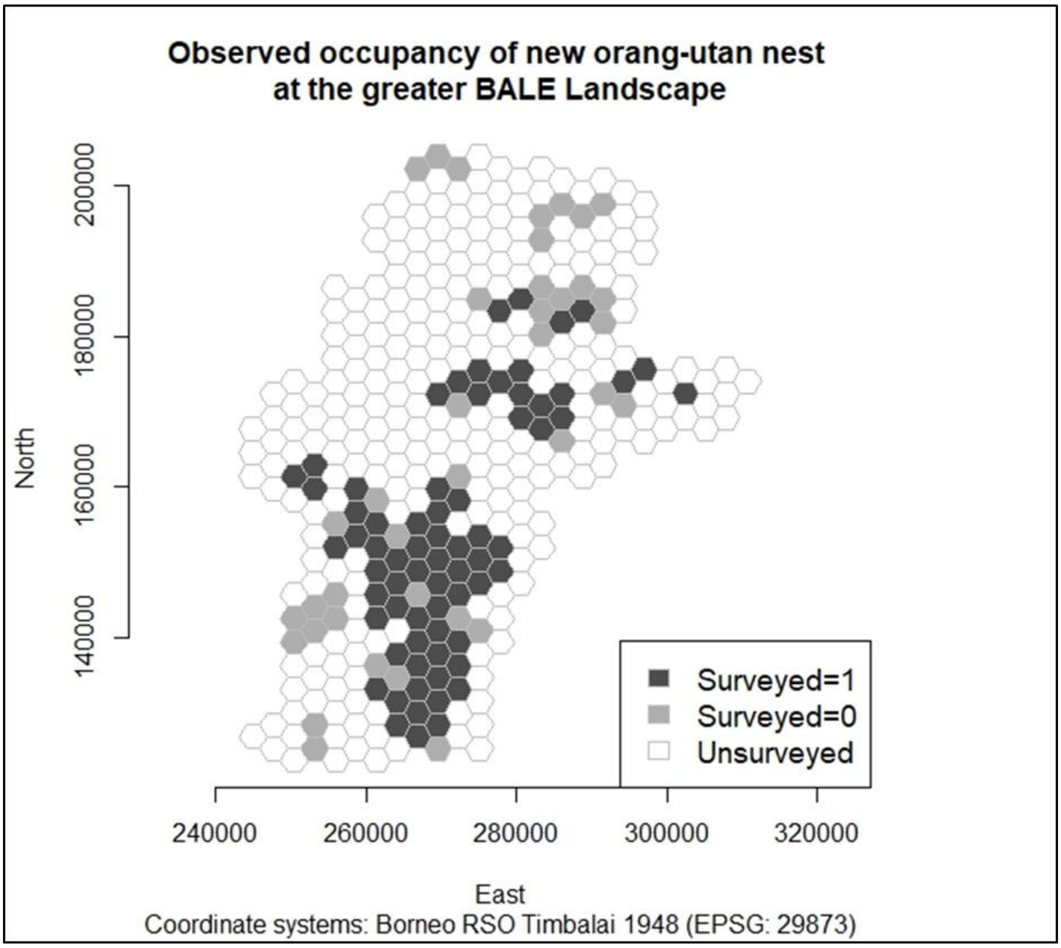

Fig. 4.1. Map showing the observed occupancy of new orangutan nest at the greater BALE landscape.

The sampling process shows: a) black hexagons as surveyed at least once and orangutan nests were detected (i.e. y = 1 for at least one new orangutan nest); b) grey hexagons as surveyed but new orangutan nests were never detected; and c) white hexagons as unsurveyed. The R source code to create the map was developed by Mike Meredith (Supplementary Appendix S4.3).

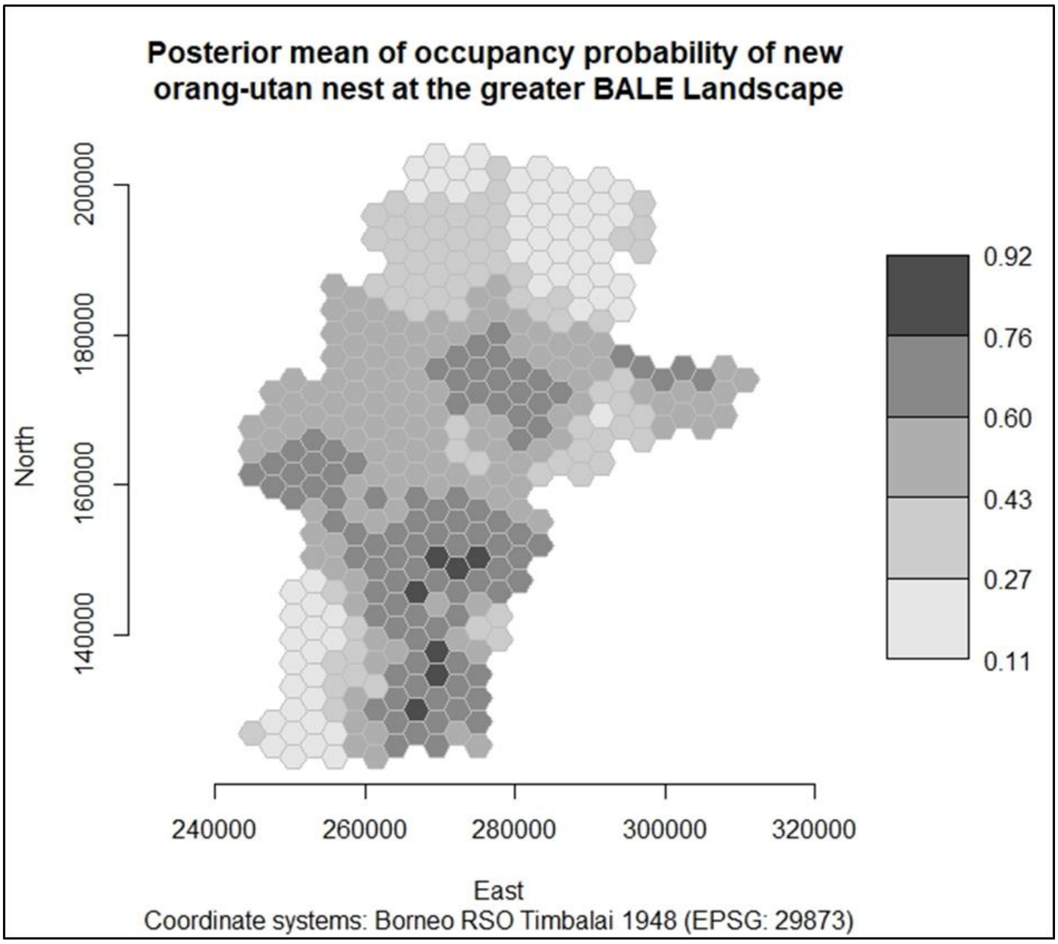

Fig. 4.2. Map showing the posterior mean of occupancy probability (ψ) of new orangutan nest for each tile at the greater BALE landscape.

The R source code to create the map was developed by Mike Meredith (Supplementary Appendix S4.3).

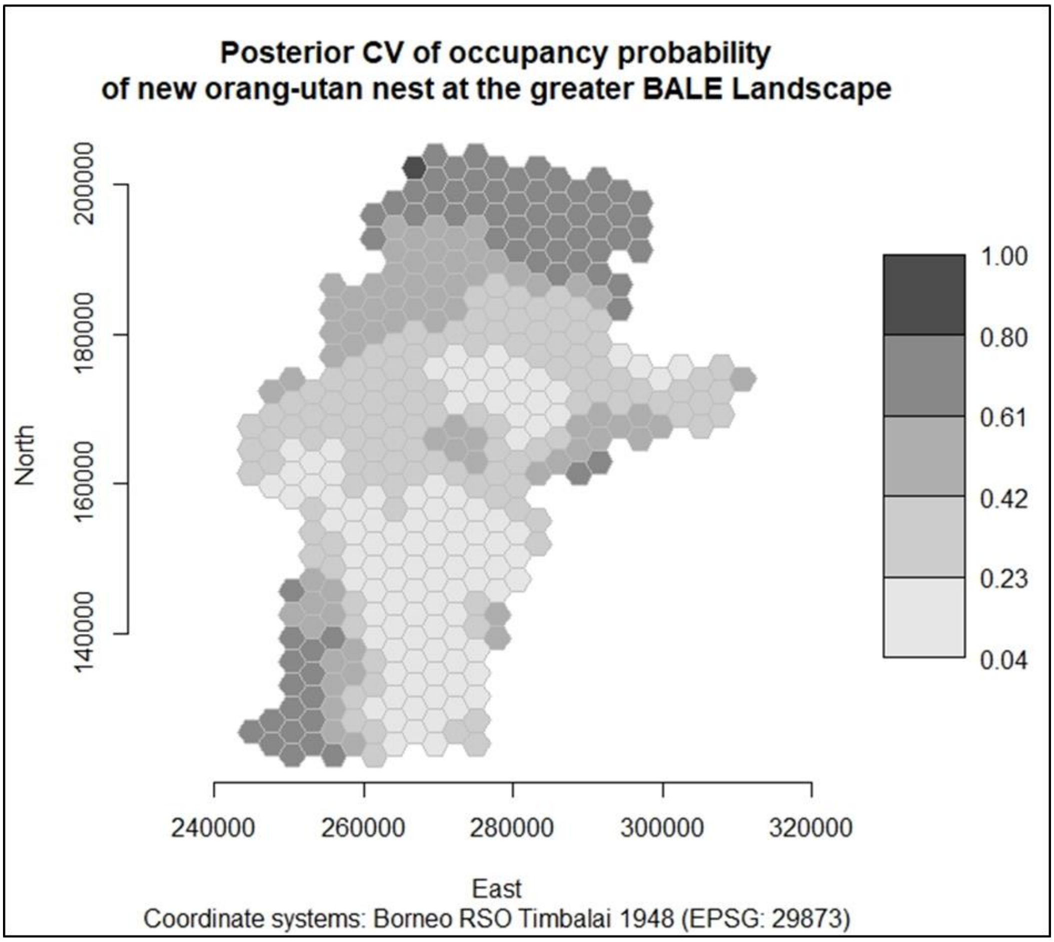

Fig. 4.3. Map showing the posterior coefficient of variation (CV) of occupancy probability (ψ) of new orangutan nest for each tile at the greater BALE landscape.

The R source code to create the map was developed by Mike Meredith (Supplementary Appendix S4.3).

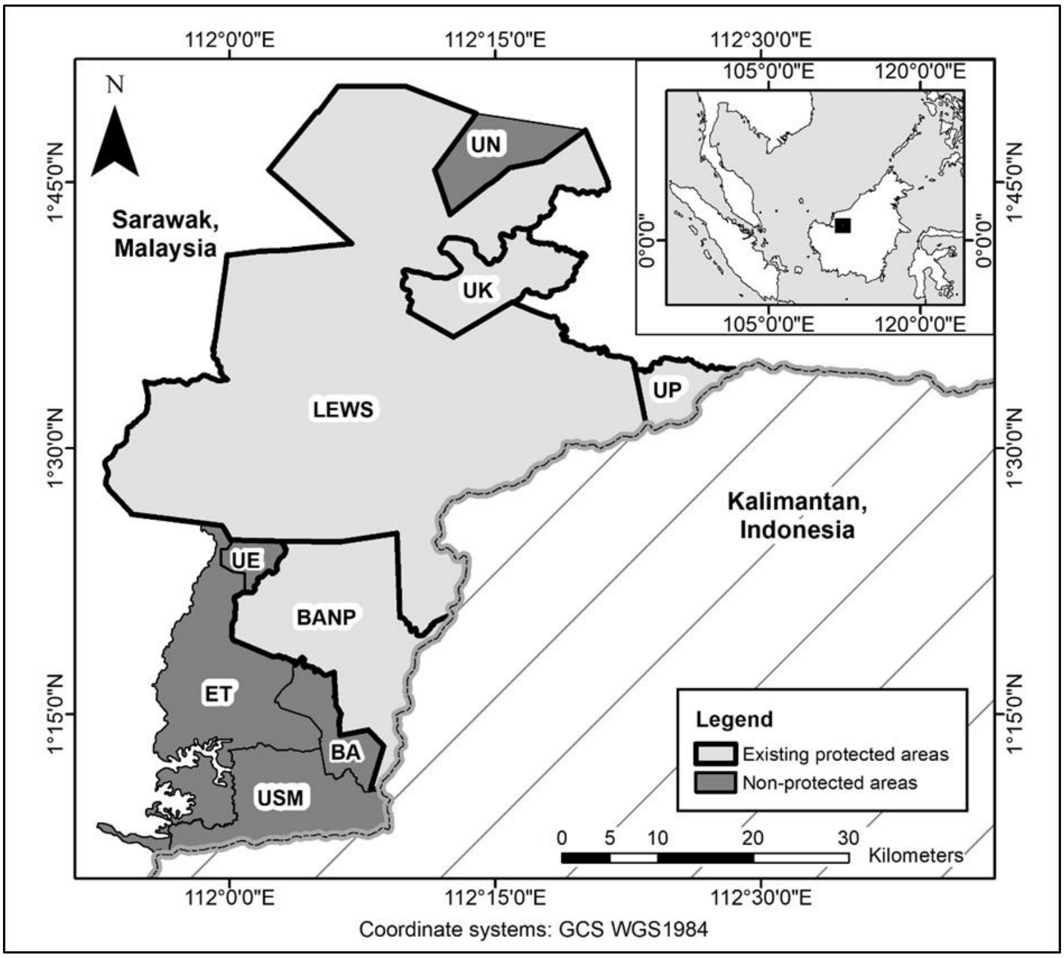

Fig. 4.4. Map showing the location of study sites.
The full name for the acronyms used is shown in Table 4.1. This map was created using the software ArcGIS 10.2.1 (www.esri.com) by JP.

Table 4.1. Orangutan conservation sites and their area sizes including core habitats and their extensions in Sarawak.
The protection status of each study site (totally protected, proposed, gazetted as extension, or non-protected) is also indicated.

Study site	Acronym	Protection status	Size (km^2)
1. Batang Ai National Park	BANP	Totally protected area	240.40
2. Lanjak-Entimau Wildlife Sanctuary	LEWS	Totally protected area	1,687.60
3. Ulu Katibas	UK	Extension of LEWS (became part of the sanctuary in 2013)	96.41
4. Ulu Pasin	UP	Extension of LEWS (became part of the sanctuary in 2013)	45.84
5. Batang Ai	BA	Proposed Southern extension of BANP	58.28
6. Ulu Engkari	UE	Proposed Northern extension of BANP	22.48
7. Ulu Ngemah	UN	Proposed extension of LEWS	69.40
8. Ulu Sungai Menyang	USM	Non-protected landscape	140.00
9. Engkari-Telaus	ET	Non-protected Community Conservation Landscape	247.80
		Total area size=	**2,608.21**

Chapter 5.

General Conclusions

In the preceding chapters, I have mentioned the main threats to the orangutans in Borneo and Sarawak, focusing on the core habitats of Batang Ai-Lanjak-Entimau (BALE) Landscape. The first step in addressing these threats is to acquire baseline data and to present them in a technical format. This is crucial in view that intervention measures for the critically endangered species vary at local and landscape levels. Thus, a comprehensive and updated report on orangutan population and distribution is essential as guidelines for park managements and other relevant agencies in deciding appropriate conservation actions for the great ape.

This final chapter summarizes the main highlights of the MPhil thesis, and brief reflections on the growing science in orangutan conservation ecology and the way forward for future collaborations. I divide the content into three sections: 1) the contribution and limitations of the research findings; 2) the direction and potential for future collaborations; and 3) a final note on the research applications beyond the core habitats of BALE Landscape.

Contribution and limitations

This MPhil thesis is written and organized in the interest of policy makers, park managers, local conservation practitioners, as well as international partners in mind. The Sarawak Government made a pledge to have zero-loss of orangutans and their habitats in the State in 2015 [1]. A Government policy on this pledge has been drafted and close to be tabled and signed off as official policy at the Sarawak State Cabinet. Therefore, the research findings presented in this manuscript are anticipated to then fuel a wider discussion and development from potential joint collaborators as part of the policy implementations. The main highlights of the contribution and limitations from this MPhil thesis are discussed below. This discussion then continues in the next section on the direction of future collaborations.

In Chapter 2, my co-authors and I described the two biggest threats to the survival of Bornean orangutans in Sarawak, which are habitat loss and intensive hunting. Identifying the direct threats to the species survival is a crucial step in achieving the goal of conserving and sustaining the orangutan population in Sarawak. We presented the threats extent based on high impact studies island-wide in Borneo by Bryan et al [2], Gaveau et al [3]. Struebig et al [4] and Santika et al [5] among others. These studies used satellite imageries to assess the extent of deforestation and forest degradation in Borneo as well as orangutan population trends. However, the satellite imagery on threats extent for Sarawak presented were of low accuracy due to limited access to official information at the time [2]. Further study is recommended to investigate the threats extent if higher accuracy data is to be used.

The recommendations made for an adaptive management of conservation actions in Chapter 2 then were based on new knowledge gained from the shortfalls in orangutan conservation in Sarawak for the past 60 years. The keys to successful conservation actions are inter-agency collaboration for enforcement and orangutan monitoring, as well as corresponding support through technological application and intelligence networks. Currently, the two main agencies that manage wildlife and protected areas in Sarawak have shown political will to achieve this. The agencies are: a) the State Government's Forest

Department Sarawak (FDS), and b) the Sarawak Forestry Corporation (SFC), a corporate entity and the operating arm of FDS. However, both agencies are presently going through major restructuring to re-define their respective roles. The Government policy on zero-loss of orangutans and their habitats is on hold pending decisions from the re-definition process.

The analyses and results based on unpublished data provided by the Wildlife Conservation Society (WCS) Malaysia complement the growing scientific repository on orangutan population studies in Borneo. In Chapter 3, the outcomes of the research show that the survey design using a Bayesian framework was a useful alternate approach for site-specific studies. The Bayesian approach is already in used in many disciplines including by Nater et al [6] to reconstruct demographic history based on genetic variation within and among the Bornean and Sumatran orangutan species. The main advantage of this approach is having all possibilities spread out as a probability distribution consistent with new data observed [7]. Possibilities that are consistent with the data gain more credibility; possibilities that are not, lose credibility. In Chapter 3, we used the Bayesian posterior distributions to infer about 95% of the most credible range of possibilities for orangutan density and population estimates. Future study is recommended to compare results and precision measurement of the Bayesian and non-Bayesian approach.

Subsequently, the strength or reliability of the results in Chapter 3 were assessed using Gimenez et al's [8] identifiability tests. Four out of the seven study sites had prior-posterior overlaps of more than 35%, which indicated that the population estimates for these sites were weak. In line with Gimenez et al and Plumptre et al [9], we recommend the following to improve estimates for future surveys: 1) more plots and revisits; 2) shorter inter-survey period of 14 to 21 days; and 3) the use of informative priors with strong reliability from nearby sites. Cole & McCrae [10] found this 35%-overlap guideline to be useful and effective for models with time series of counts such as capture-recapture models and occupancy models. We came to a similar conclusion for our *N*-mixture model. Furthermore, WCS Malaysia has begun to incorporate identifiability tests into ongoing orangutan studies.

We continued the analyses of unpublished data provided by WCS Malaysia in Chapter 4. The academic exercise showed that the occupancy modelling based on detection-nondetection of new nest data could be used as proxies to map orangutan distribution. This study aimed to address the possible overestimation of orangutan population and their projected decline numbers due to extrapolation of orangutan density in areas perceived to be 'suitable habitats' but potentially not occupied by orangutans. Future study is recommended to compare this study design with other methods such as the species distribution modelling. The areas of comparison could include cost-effective measures, spatial spread of data points, and the incorporation of other types of presence data derived from calls, direct sightings, drone images, and manned aircraft images, among others.

The unreasonably high probability of detection and variability or uncertainty in the posterior coefficient of variation (CV) showed that much adjustments are needed to fine-tune our sampling scheme. This includes applying Mackenzie & Royle's [11] suggestions to conduct fewer surveys at more sites, in a shorter timeframe or sampling season for future surveys. Mackenzie & Royle asserts that these adjustments improve the study design and are more suitable for rare species with low occurrence, such as orangutans as in our context.

Future direction
The lessons learned covered in Chapter 2 showed that there is room to improve conservation efforts in Sarawak. We described that the way forward for orangutan conservation is through inter-agency collaboration, technological application, community livelihood development, and increased public support. Steps are already taken by the Sarawak Government to partner with various stakeholders to conduct joint enforcement with successful prosecution of six non-Malaysians in April 2018 [12]. Since the 2015 pledge, both FDS and SFC have invested time and resources to improve surveillance on encroachment using drones and small aircraft equipped with high resolution cameras and sensors [13]. FDS is also working alongside various stakeholders to empower villagers to be more self-sustaining through community livelihood programs [14]. Furthermore, public and corporate events such as the 'Run for the wild' are jointly organized to engage the urban public to support sustainable environmental policies [15].

On the research front, WCS Malaysia and SFC continues to jointly monitor orangutan population and distribution at known habitats in Sarawak. Both organizations have signed a Memorandum of Understanding (MoU) to work at the *Research for Intensified Management of Bio-Rich Areas* or RIMBA Sarawak study sites in 2015. Some of the recommendations for future studies as outlined in Chapters 3 and 4 are jointly carried out at the point of writing. Trainings are ongoing for SFC rangers and senior field assistants on data collection at these sites. There is also a potential study to incorporate aerial or drone data to improve the accuracy of orangutan nest counts used in the population and distribution analyses. Wich [16] pilot-tested this in Sabah but this have yet to peak interest in Sarawak.

A final note
This MPhil thesis has highlighted the importance of the core habitats of BALE Landscape for orangutan conservation ecology in Sarawak. The Landscape has an estimate of 1,278 to 2,363 orangutans based on the combined results of Chapter 3 and Wich et al [17]. This makes the contiguous protected and non-protected areas of the greater BALE Landscape, home to the most viable orangutan populations in Sarawak. The unpublished data and subsequent results presented here were also one of the most comprehensive and site-specific studies on wild orangutans by the WCS Malaysia since the 1990s. Conservation efforts are ongoing and are being scaled up over time to ensure the survival of the critically endangered species. It is anticipated that the next comprehensive population studies at the core habitats to be conducted in the next 5-10 years. This is due to the biological nature of the orangutans being one of the slowest-breeding mammals on Earth [18]. The results from this thesis is being planned to be presented in a more understandable format to conservation partners of WCS Malaysia in view of the technicality of its content.

In the meantime, future studies are expected to expand to include the lesser known remnant habitats of Sedilu-Sebuyau-Lesong Landscape. The fragmented habitats are located approximately 120 km to the west of the BALE Landscape. Sedilu, Sebuyau and Lesong have historical values for being the sites where: a) Wallace [19] and Hornaday [20] collected their orangutan specimens as indicated in Chapters 1 and 2; b) Schaller [21] conducted the first orangutan population study using nests as proxies; and c) Harrisson [22] wrote about her journey into the jungle that became pilot sites for a discontinued orangutan reintroduction program in the 1970s. WCS Malaysia and their partners aim to increase the conservation values of the Sedilu-Sebuyau-Lesong Landscape and to extend legal protection status for areas around them. This is to be carried out potentially by applying the study designs presented in Chapters 3 and 4 to report on the orangutan status at these remnant habitats.

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Chapter 2: Threats and lessons learned from past orangutan conservation strategies in Sarawak, Malaysia

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Chapter 3. Population estimates of Bornean orangutans using Bayesian analysis at the greater Batang Ai-Lanjak-Entimau landscape in Sarawak, Malaysia

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Chapter 4. Occupancy modelling of orangutan distribution at the greater Batang Ai-Lanjak-Entimau landscape in Sarawak, Malaysia

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Chapter 5. General Conclusions

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Supplementary Materials

Chapter 3. Population estimates of Bornean orangutans using Bayesian analysis at the greater Batang Ai-Lanjak-Entimau landscape in Sarawak, Malaysia

Supplementary Appendix S3.1: Additional data and results.

Supplementary Table S3.1. Overview of plots surveyed and reserved for the study sites. The site where the survey teams had to use the reserves is highlighted in grey.

Study site	No. of plots surveyed	No. of plots reserved	Surveyed plot ID	Reserved plot ID
Southern (Batang Ai)	3	5	A,B,C	D,E,F,G,H
Northern (Ulu Engkari)	3	2	I,J,K	L,M
Ulu Ngemah	3	2	N,O,P	Q,R
Ulu Katibas	5	0	S,T,U,V,W	-*
Ulu Pasin	3	2	X,Y,Z	AA,AB
Ulu Sungai Menyang	6	1	A1,B1,C1,D1,E1,F1	G1**
Engkari-Telaus	6	1	A2,B2,C2,D2,E2,F2	G2**
Total:	**29**	**13**		

Notes:

*As two of the reserves were used (Plots V and W), they are not indicated under the column 'Reserved plot ID'.

**Plots G1 and G2 were not surveyed as permission was not granted by local communities.

Supplementary Table S3.2. Details for three repeat surveys conducted at the study sites at the greater BALE landscape. Coordinate system: Timbalai 1948 (RSO Borneo Meters).

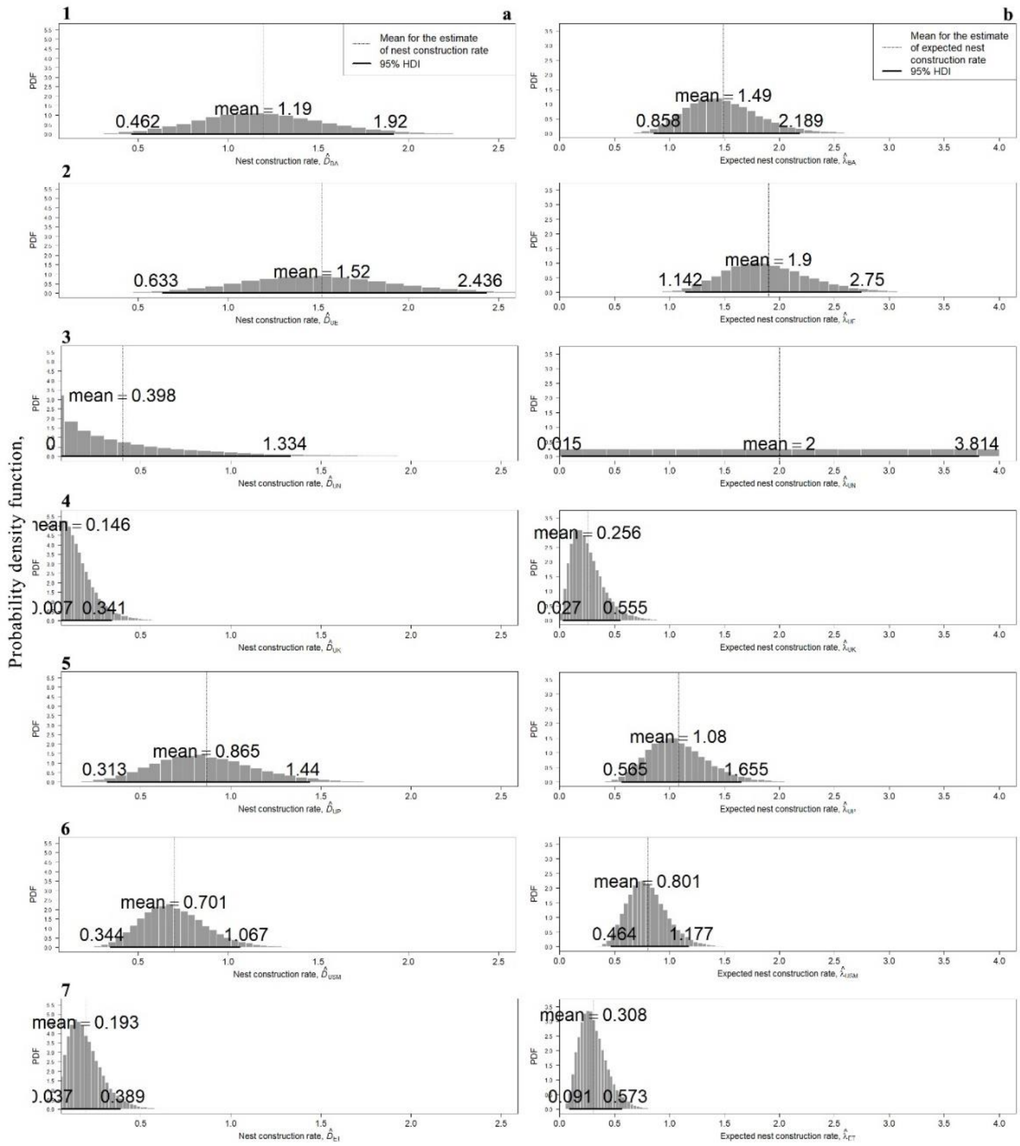
Plot	Area	Location	GPS coordinates for the centre of each plot		Dates for repeat surveys			Num. of days, t	New nests recorded on the first survey, x	Total new nests on second and third surveys, y	Sign of orangutan nest (old/ new), z	Plot size, a (km^2)
			Easting (m)	Northing (m)	First	Second	Third					
A	BA	Nanga Senyumboh	271059	135000	18 & 19 Mar. 2011	8 Apr. 2011	29 Apr. 2011	40	2	7	1	0.1563
B	BA	Mawang-Wong Tibang	267334	134560	22 & 23 Mar. 2011	11 Apr. 2011	3 May 2011	40	10	9	1	0.1552
C	BA	Semuban	266527	140567	26 & 27 Mar. 2011	14 Apr. 2011	6 May 2011	40	2	6	1	0.1474
I	UE	Engkramoh Ulu	262079	153833	7 & 8 Jul. 2011	30 Jul. 2011	20 Aug. 2011	42	0	6	1	0.1464
J	UE	Engkramoh Ili	259925	152962	12 & 13 Jul. 2011	1 Aug. 2011	22 Aug. 2011	39	2	9	1	0.1446
K	UE	Segrak	259080	155009	18 & 19 Jul. 2011	5 Aug. 2011	25 Aug. 2011	37	0	11	1	0.1384
N	UN	Empurau	289818	196553	12 & 13 Nov. 2011	-	-	2	NA	NA	0	0.1448
O	UN	Pang	284175	196558	10 Dec. 2011	-	-	1	NA	NA	0	0.1483
P	UN	Semujan	283378	193744	16 Dec. 2011	-	-	1	NA	NA	0	0.1442
S	UK	Likau	291331	184295	17 & 18 Feb. 2012	-	-	2	NA	NA	0	0.1544
T	UK	Katibas	285377	183037	21 & 22 Feb. 2012	-	-	2	NA	NA	0	0.1643
U	UK	Datai	287468	184320	25 & 27 Feb. 2012	19 Mar. 2012	7 Apr. 2012	42	1	1	1	0.1434
V	UK	Nyungan	284482	181015	13 & 15 Mar. 2012	4 Apr. 2012	25 Apr. 2012	40	4	1	1	0.1465
W	UK	Begua	282162	184228	17 & 18 Mar. 2012	6 Apr. 2012	-	19	0	0	1	0.1269
X	UP	Bloh Karoh	301123	172139	19 & 20 Jul. 2012	10 Aug. 2012	1 Sep. 2012	42	1	7	1	0.1440
Y	UP	Selemas	303123	172139	21 & 22 Jul. 2012	13 Aug. 2012	3 Sep. 2012	41	4	5	1	0.1496
Z	UP	Selemas	302982	172487	25 & 26 Jul. 2012	16 Aug. 2012	5 Sep. 2012	40	0	4	1	0.1566
A1	USM	Genting Badak	268196	127059	22 & 23 Mar. 2014	13 Apr. 2014	4 May 2014	43	0	2	1	0.1248
B1	USM	Kasai	268628	131014	29 & 30 Mar. 2014	15 Apr. 2014	6 May 2014	38	3	6	1	0.1371
C1	USM	Jambu	265456	131678	2 & 3 Apr. 2014	16 Apr. 2014	8 May 2014	36	1	6	1	0.1387
D1	USM	Ulu Jirak	262849	128260	13 & 14 Mar. 2015	8 Apr. 2015	1 May 2015	49	4	4	1	0.1507
E1	USM	Sumpa	261248	133965	6 & 7 Apr. 2015	27 & 28 Apr. 2015	22 May 2015	46	2	4	1	0.1445
F1	USM	Kedang Katik	253358	126012	20 & 21 Oct. 2013	11 Nov. 2013	1 Dec 2013	42	0	0	1	0.1441

Plot	Area	Location	GPS coordinates for the centre of each plot		Dates for repeat surveys			Num. of days, t	New nests recorded on the first survey, x	Total new nests on second and third surveys, y	Sign of orangutan nest (old/ new), z	Plot size, a (km²)
			Easting (m)	Northing (m)	First	Second	Third					
A2	ET	Nanga Suga	255082	144128	22 & 23 Sep. 2014	15 Oct. 2014	-	22	0	0	1	0.1575
B2	ET	Engkramoh	255898	151829	13 & 14 Apr. 2015	14 Apr. 2015	25 May 2015	42	1	3	1	0.1409
C2	ET	Senibong	262841	137065	13 & 14 Mar. 2015	11 Apr. 2015	3 May 2015	51	2	2	1	0.1475
D2	ET	Tisau Ulu	252726	142431	22 & 23 Oct. 2014	-	-	1	NA	NA	0	0.1595
E2	ET	Sungai Tutong	250149	141145	28 & 29 Oct. 2014	-	-	1	NA	NA	0	0.1519
F2	ET	Ukap	262022	142650	19 & 20 Mar. 2015	13 Apr. 2015	5 May 2015	46	1	0	1	0.1569
				Total=	**29**	**22**	**20**	**-**	**40**	**93**	**22**	**4.2654**

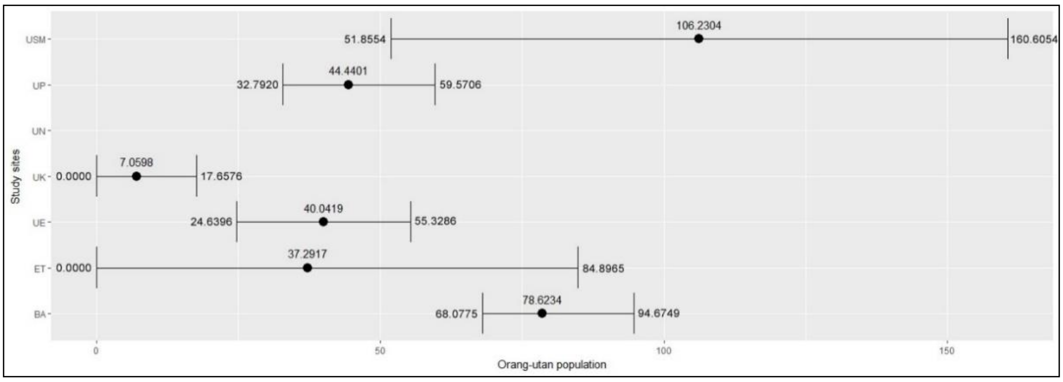
Note: There were no repeat surveys conducted on the second and third occasions for Plots N, O, P, S, T, D2 and E2 (shown as '-') as there was no sign of orangutan nest (old/new) in the plots. In results for y, 'NA' refers to no sign of orangutan nests (old/new) at the plot, and '0' refers to old orangutan nests detected at the plot but no new nests recorded.

Supplementary Table S3.3. Estimates of nest construction rate, $\hat{D}$ (nests km^{-2} day^{-1}), expected nest construction rate if whole study site is used by orangutans ($\hat{\lambda}$), and probability of old nest at a site ($\hat{\psi}$) with 95% highest density interval (HDI) for the study sites at the greater BALE landscape.

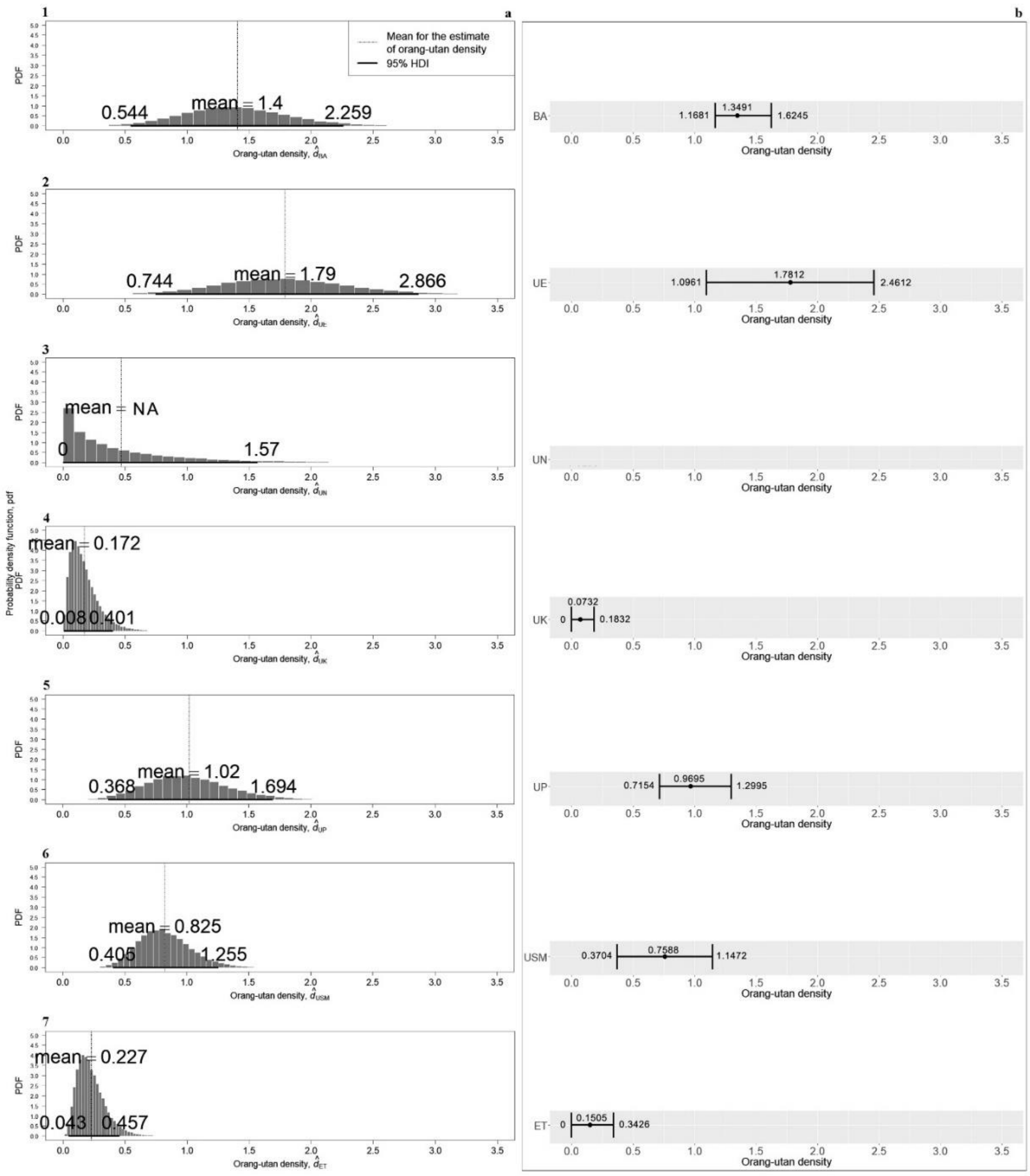
		Estimated nest construction rate (given plot use by orangutans)			**Expected estimate of nest construction rate**			**Estimated probability of old nest at a site**		
Study site	**Area**	$\hat{D}$	**Lower HDI**	**Upper HDI**	$\hat{\lambda}$	**Lower HDI**	**Upper HDI**	$\hat{\psi}$	**Lower HDI**	**Upper HDI**
Southern (Batang Ai)	BA	1.1942	0.4624	1.9198	1.4905	0.8585	2.1889	0.8011	0.4765	1.0000
Northern (Ulu Engkari)	UE	1.5206	0.6326	2.4363	1.9008	1.1423	2.7501	0.8003	0.4743	1.0000
Ulu Ngemah	UN	0.3979	0.0000	1.3342	1.9988	0.0148	3.8142	0.1995	0.0000	0.5269
Ulu Katibas	UK	0.1461	0.0068	0.3412	0.2559	0.0273	0.5552	0.5715	0.2381	0.8986
Ulu Pasin	UP	0.8648	0.3130	1.4402	1.0814	0.5653	1.6554	0.8000	0.4699	1.0000
Ulu Sungai Menyang	USM	0.7008	0.3444	1.0671	0.8009	0.4641	1.1769	0.8750	0.6497	1.0000
Engkari-Telaus	ET	0.1932	0.0369	0.3885	0.3082	0.0908	0.5735	0.6265	0.3250	0.9267



Supplementary Fig. S3.1. The columns correspond to the probability density function of: a) estimated nest construction rate, $\hat{D}$ (nests km^{-2} day^{-1}) and b) expected estimate of nest construction rate ($\hat{\lambda}$) with 95% HDI at the study sites. The row sequence corresponds to the study sites: 1) Batang Ai, 2) Ulu Engkari, 3) Ulu Ngemah, 4) Ulu Katibas, 5) Ulu Pasin, 6) Ulu Sungai Menyang, and 7) Engkari-Telaus.



Supplementary Fig. S3.2. Orangutan population estimates based on a non-Bayesian approach with 95% confidence interval (CI). The combined point estimate using this approach was 313 orangutans with 177-472 as 95% confidence interval. We conducted bootstrapping analysis with 100,000 random sampling with replacement of the original datasets shown in Supplementary Table S3.2. The methodology for the analysis was adapted from Ancrenaz et al [1]. The confidence interval here is shown as a line with two end points as the results do not correspond to a probability distribution, but based on a sampling distribution with area under the curve that do not integrate to 1.



Supplementary Fig. S3.3. Estimated orangutan density (individual km^{-2}) based on the: a) Bayesian method with 95% HDI, and b) non-Bayesian approach with 95% CI. The row sequence corresponds to the study sites: 1) Batang Ai, 2) Ulu Engkari, 3) Ulu Ngemah, 4) Ulu Katibas, 5) Ulu Pasin, 6) Ulu Sungai Menyang, and 7) Engkari-Telaus. The lower limit of orangutan density ranges at sites with low counts of new nest should be > 0. However, the bootstrap analysis (non-Bayesian approach) could not compute low counts of new nests at sites UK and ET, resulting in 0 included within the 95% CI. This is incorrect as there were new nests recorded, meaning at least 1 orangutan was present at each site at the time of survey.

Supplementary Appendix S3.2: Background of study sites, and location of surveyed plots and new orangutan nests at the study sites.

Background of study sites

Malaysia comprises of three regions: Peninsular Malaysia, Sabah and Sarawak. It is in the latter two regions that orangutans are found. In Sarawak, orangutans are only found in two locations: the Batang-Ai-Lanjak-Entimau (BALE) landscape where the main populations are found and the Gunung Lesong-Ulu Sebuyau-Sedilu landscape where the remnant populations are still sighted. Orangutans are not found in other areas including Maludam National Park, even after surveys in 1985, 1987, 1988, 1990 and 1994 [2,3] and the exhaustive 18-month research in the area between 2002 and 2004 [4,5]. There were reports of orangutan sightings in the past 10 years at Bungo Range National Park, Sabal Forest Reserve and the proposed Klingkang Range National Park. Researchers from the WCS Malaysia conducted rapid assessments to document orangutan signs at these areas in 2016 and 2017 but no signs detected to date.

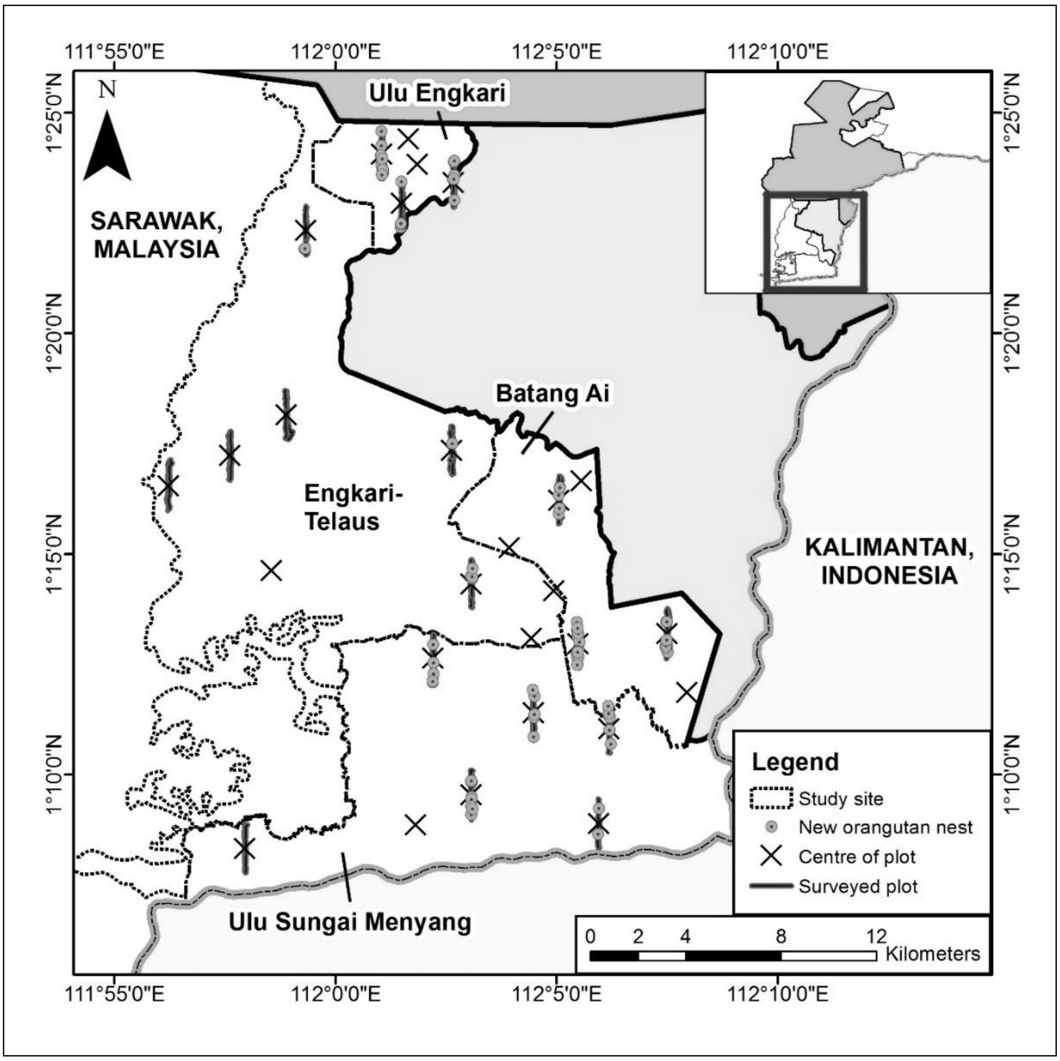
The BALE landscape consists of two contiguous protected areas, namely the Batang Ai National Park (BANP) and the Lanjak-Entimau Wildlife Sanctuary (LEWS). The greater BALE landscape then consists of seven areas: five proposed extension areas (at the time of survey) [6] and two non-protected landscapes. After completing surveys at Ulu Katibas and Ulu Pasin, both areas were successfully gazetted as extensions to Lanjak-Entimau Wildlife Sanctuary in May 2013.

Prior to the surveys, anecdotal information shows that there were orangutan sightings in Ulu Ngemah, Ulu Katibas and Ulu Pasin [6]. These areas were then considered for potential extensions to reduce commercial exploitation and encroachment into lands with community rights [6]. Although the areas consist of native forests, they could have been alienated for development, be it for logging, or large-scale agriculture, as they were not part of LEWS. The three extension areas of LEWS are important for conservation as the current boundary is a cut line and does not follow natural ridgelines or the water catchment.

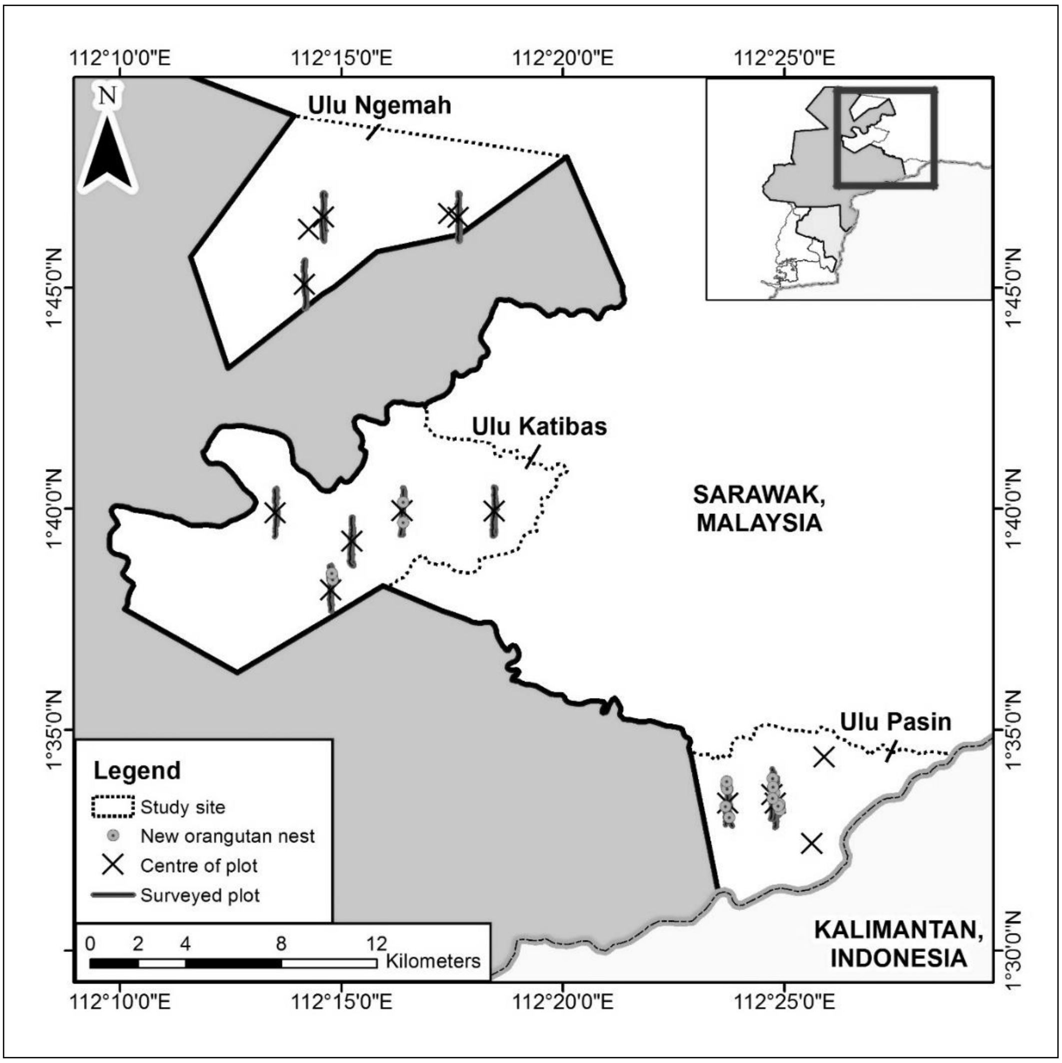
Similarly, in Batang Ai National Park, orangutans were frequently sighted in the two sites outside the park: the proposed Southern extension (Batang Ai) and the Northern extension (Ulu Engkari) [7]. The proposed additions to Batang Ai National Park or proposed conservation areas were significant for conservation based on prior evidence of orangutan presence in these places [7]. Rapid assessments carried out at Batang Ai in 2003 showed that the highest concentration of orangutan nest surveyed was located there [8]. Repeat surveys in Lanjak-Entimau Wildlife Sanctuary along the periphery of Ulu Engkari also revealed significant number of orangutan nests in the area [8].

Since 2012, researchers jointly conducted rapid assessments of new orangutan nests at the Ulu Sungai Menyang landscape (2012 and 2013) and the Engkari-Telaus Community Conservation Landscape (2014) under the Heart of Borneo (HoB) Initiative [9]. The surveys conducted in the two non-protected landscapes were the direct result of threats from large-scale land use conversion. Licenses to log both landscapes were not renewed by the Director of Forests with directives from the State's Second Minister of Resource Planning and Environment (the Chief Minister of Sarawak has since renamed this ministry as 'Ministry of Urban Development and Natural Resources' in 2017).

The combined total area of the seven study sites is 680.21 km^2.



Supplementary Fig. S3.4. Location of surveyed plots and new orangutan nests at Ulu Engkari, Batang Ai, Engkari-Telaus and Ulu Sungai Menyang. The study sites are contiguous with the core habitats of Batang Ai National Park (light grey) and Lanjak-Entimau Wildlife Sanctuary (dark grey). Coordinate system: GCS WGS 1984 (WGS 1984). This map was created using the software ArcGIS 10.2.1 (www.esri.com) by SN and JP.

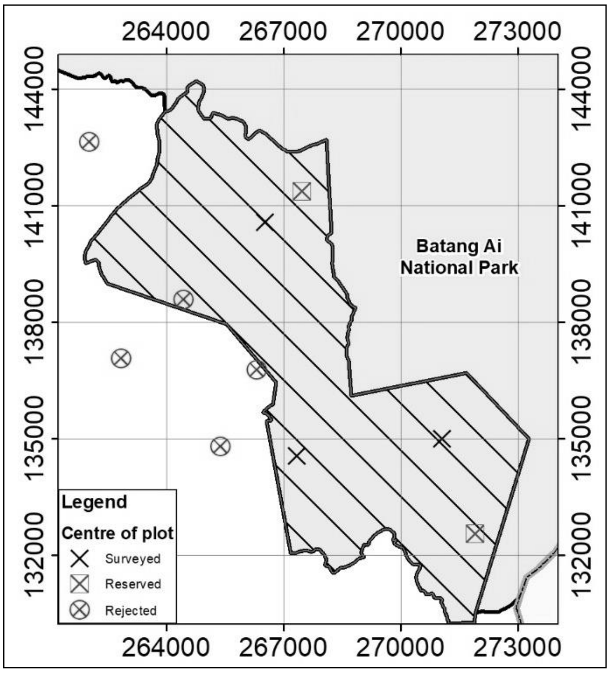


Supplementary Fig. S3.5. Location of surveyed plots and new orangutan nests at Ulu Ngemah, Ulu Katibas and Ulu Pasin. The study sites are contiguous with the core habitat Lanjak-Entimau Wildlife Sanctuary (dark grey). Coordinate system: GCS WGS 1984 (WGS 1984). This map was created using the software ArcGIS 10.2.1 (www.esri.com) by SN and JP.

Supplementary Appendix S3.3: Additional method description.

a) Plot layout

We selected the centre for each plot (both easting and northing) at random using `=RANDBETWEEN(bottom, up)` function in MS Excel. The values for `(bottom, up)` were the edges of a rectangular connecting the boundary edges of the extension area. If the randomly selected centre of plot fell outside the study area, it was rejected. Only plot centres inside the study site and at least 1 km away from nearby protected areas or boundary of the study site were selected.



Supplementary Fig. S3.6. The proposed Southern extension of Batang Ai National Park (hatching). Coordinate system: Timbalai 1948 (RSO Borneo Meters). This map was created using the software ArcGIS 10.2.1 (www.esri.com) by SN and JP.

Each plot consists of four strips 36 m in width and 1 km in length arranged in a north-south direction. A trail or *rentis* was marked along the centre line of each strip before the surveys commenced. The survey extended 18 m from each side of the *rentis*. The use of 18 m half-width for the plot was derived from previous surveys using Distance sampling at the Batang Ai-Lanjak-Entimau (BALE) landscape between 2003 and 2007 whereby the effective strip-half-width was 18 m.

We identified four strips by their positions: Northwest, Northeast, Southwest and Southeast respectively. The rationale of having four strips was to increase survey effort in one plot and save travelling time between plots, instead of having multiple two-strip plots situated far apart from each other.

The sampling scheme of this study design included the following:

i. All the plots were named alphabetically. The order of the alphabets operates as the sequence for travelling between plots (where possible);
ii. Surveys were conducted at no less than three plots with sign of orangutan nest (old/new);
iii. If one of the plots had no sign of nests, the reserve plot would be surveyed. This was only limited to the two reserve plots;
iv. Surveys were stopped (no second and third surveys) if all the three original plots or six original plots had no sign of any orangutan nest (old/new). The three original plots refer to Batang Ai (BA), Ulu Engkari (UE), Ulu Ngemah (UN), Ulu Katibas (UK) and Ulu Pasin (UP). But subsequently, we realized that a minimum of three plots for each study site were too few. Therefore, we opted to increase original plots to be surveyed to six plots for Ulu Sungai Menyang (USM) and Engkari-Telaus (ET). Surveys were also stopped if three plots (or six plots for USM and ET) with the two reserves (due to absence of orangutan nests in one or two of the original plots) had no sign of orangutan nest (old/new)*;

v. Given budgetary constraints, labour restrictions and limited time, the maximum numbers of plots that could be surveyed were up to five for BA, UE, UN, UK and UP, and up to seven plots for USM and ET.

*NOTE: The actual sampling scheme was as follows: only three plots were surveyed at BA, UE, UN and UP, five plots at UK, and six plots each for USM and ET. No orangutan nest (new or old) was observed during the first survey at Plots S and T in UK (Supplementary Table S3.1). These two plots were then designated as not having used by orangutans and not resurveyed. Meanwhile, new orangutan nest was recorded at the third plot (U) on the first survey at UK. Therefore, two reserved plots (Plots V and W) were surveyed in replacement for Plots S and T. New orangutan nests were seen in these reserved plots at UK. The plots at UN were discontinued altogether as no new or old orangutan nests were recorded in all three plots (N, O and P).

b) First survey

We surveyed each strip thoroughly twice, with two separate teams walking in opposite directions. The manner for the search was: Team 1 surveyed Strip-NW first, and then re-surveyed by Team 2 from the opposite direction on the same day. Meanwhile, Team 2 surveyed Strip-NE first, and then by Team 1 from the opposite direction. The same applies for Strip-SW and Strip-SE by both teams (Supplementary Fig. S3.7).

We recorded new orangutan nests within the strips (18 m each side of the *rentis*) and clearly tagged the trees that had these nests. Wich & Boyko [10] noted that 'there was a sharp drop in nest detection after 10 m on either side of the line transect', and 'nests beyond 10 m were found less than half the time by every team'. However, it must also be noted here that Wich & Boyko's line transect method required the survey teams to stay on the *rentis*, while the plot count method for this project allowed the survey teams to fan out up to 18 m on either side. As such, the drop in nest detection after 10 m on either side of the one transect was not violated or relevant. Perpendicular distance (PPD) from the new nest to the centre line (*rentis*) was measured for verification. New orangutan nests that were visible outside the strip were also recorded into the datasheet but not used for data analysis. The information was useful during subsequent surveys as a reference to avoid recording trees with new orangutan nests that were outside the strip.

The reasons for two teams on the first survey were: (a) to increase the probability of detecting all the orangutan nests, and (b) to evaluate the assumption that all new nests were detected on a single search. New nests recorded on the first surveys were included in an analysis to assess q. These new nests were however not included in analyses of nest construction rate or for calculating the density of orangutans in the plots as it was not known when these nests were constructed.

The two teams were not independent, as the first team tagged trees where they detected new nests. The second team could see the tagged trees and searched for, and recorded any additional new nests which the first team did not record.

Supplementary Table S3.4. Formula to evaluate assumption that all new nests were detected on a single search. Given: q is the probability of detecting new nest by two teams on the first survey, and; x is the number of new nests detected during the first surveys at each of the plots**.**

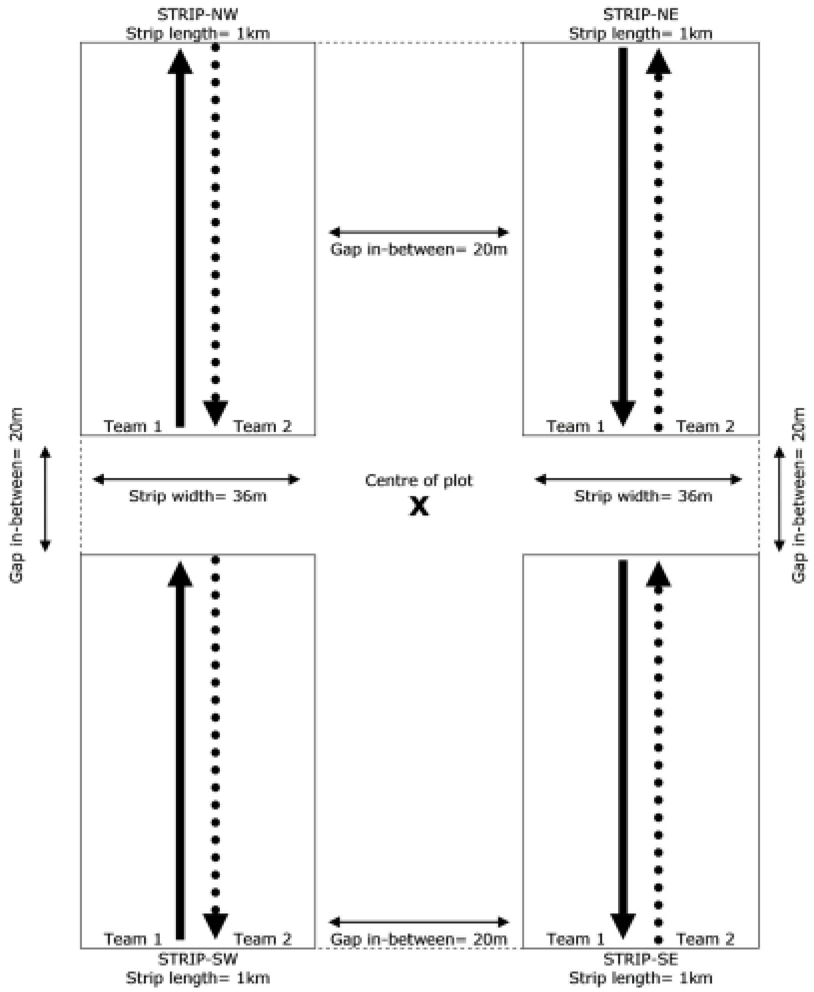
	Description of first survey	**Probability of detection**	**Estimated number of new nests detected during first surveys**
i.	New nest detected by the first team	q	$(q)\,x$
ii.	New nest missed by the first team, but detected by the second team	$(1 - q)\,q$	$(1 - q)\,(q)\,x$
iii.	New nest missed by the second team	$(1 - q)\,(1 - q)$	$(1 - q)\,(1 - q)\,x$

Orangutan nests were described into two broad categories for this project: a new orangutan nest has green leaves (at least one green leaf), whereas an old orangutan nest is without green leaf. The two categories were further classified into four decay classes (Class A to Class D). During the surveys, only new nests (with green leaves), that is Class A and Class B nests, were recorded and used for data analysis.

Supplementary Table S3.5. Decay classes and categories for orangutan nests adapted from van Schaik et al.[11].

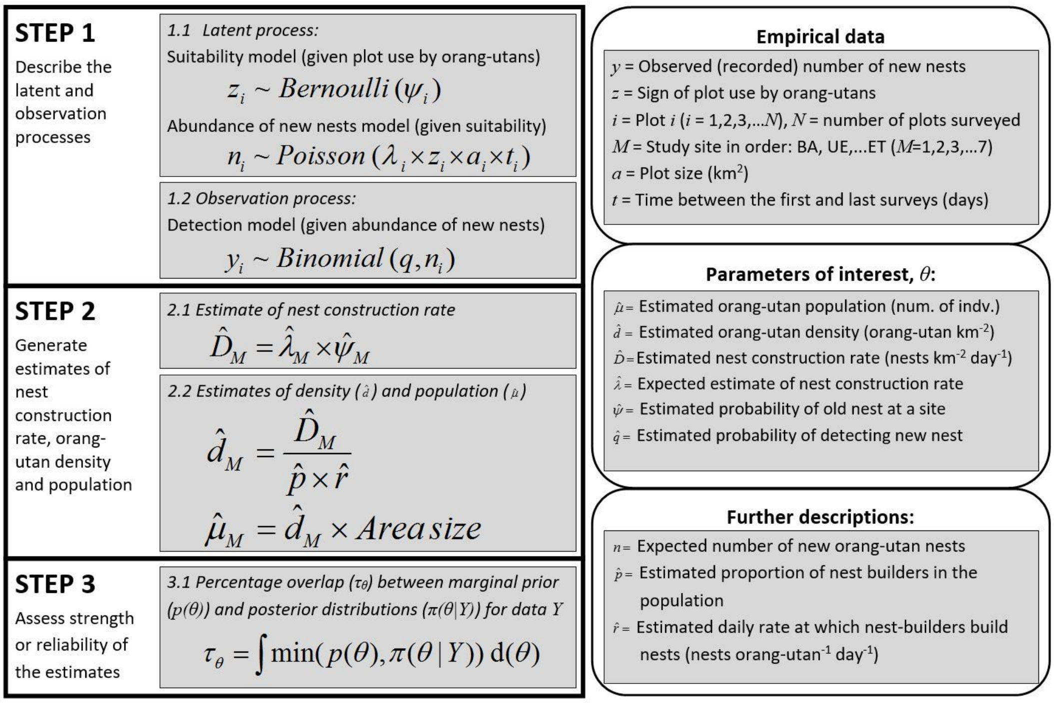
Class	Nest category		Description
A	*With green leaves*	:	New; leaves are still green
B		:	New but decaying; leaves may still be attached, and the nest is still firm and solid
C	*No green leaf*	:	Old; leaves are gone and holes are visible in the nests
D		:	Very old; twigs and branches are still present, but no longer in the original shape of the nest

c) Second and third surveys
We conducted the second and third surveys for each plot at intervals of approximately 21 days. Each strip was only surveyed once by a single team as *q* was already estimated. The team searched the whole area for new nests and there was no second team to repeat the survey in the opposite direction. The same process was repeated for the third survey. The lead researchers for all the teams were the same throughout the project.



Supplementary Fig. S3.7. Diagram of four strips in one plot.

Supplementary Appendix S3.4: The 3-step guide to analysing the *N*-mixture models using a Bayesian framework.



Supplementary Fig. S3.8. Overview of the three-step guide to analysing the *N*-mixture models using a Bayesian framework [12] to generate estimates of nest construction rate, orangutan density and population. The strength or reliability of the estimates was assessed using an identifiability test [13].

Supplementary Appendix S3.5. Data analysis (grey cells) and selected outputs (white cells) using JAGS in R.

Introduction

We used the Just Another Gibbs Sampler (JAGS) [14] in R [15] to perform the Markov chain Monte Carlo (MCMC) computation in the Bayesian analysis to generate the following:

1. Estimates of orangutan population (mu.hat or $\hat{\mu}$), density (d.hat or $\hat{d}$) and probability of old nest at a site (psi or $\hat{\psi}$) with 95% highest density interval (HDI).
2. Histograms of the posterior outputs.

We surveyed seven study sites. The analysis sequence and results for this Appendix were in chronological order of the surveys, namely: 1. Batang Ai (BA); 2. Ulu Engkari (UE); 3. Ulu Ngemah (UN); 4. Ulu Katibas (UK); 5. Ulu Pasin (UP); 6. Ulu Sungai Menyang (USM); 7. Engkari-Telaus (ET).

Data analyses using the Bayesian framework

Objective #1: To generate estimates of orangutan population (mu.hat or $\hat{\mu}$), density (d.hat or $\hat{d}$) and probability of old nest at a site (psi or $\hat{\psi}$) with 95% highest density interval (HDI).

1.1. Load R packages and retrieve data

Load two R packages for the analyses, namely: the `R2jags` package developed by Su & Yajima [16]; and the `wiqid` package developed by Meredith [17].

```
library(R2jags)
citation(package="R2jags")
library(wiqid)
citation(package="wiqid")
```

Retrieve the data shown in Supplementary Table S3.2 in .csv format. Area sizes in km^2 for the study sites are assigned in chronological order of the surveys (BA, UE, UN, UK, UP, USM, ET). The number of nest built per orangutan per day is based on Ancrenaz et al's [1] as previous orangutan follows were unsuccessful to determine $\hat{p} \times \hat{r}$ in the BALE landscape.

```
nests.Data.ALL <- file.choose()  # Retrieve data in .csv format
Area.ALL <- c(58.28, 22.48, 69.40, 96.41, 45.84, 140.00, 247.80)
p.hat_r.hat = 0.8500
```

1.2. Run model

Assign a `set.seed` to specify, save and restore the model. Priors used are broad uniform for $\hat{x}_0$, and `dbeta(5,1)` for *q*, that is to skew the distribution towards 1 in the probability density function. Details of the model are given in the Methods section of the chapter and an overview of the 3-step guide to analysing the *N*-mixture models is shown in Supplementary Fig. S3.8.

```
set.seed(123)
sink("model.txt")
cat("
model {
       # PRIORS:
       x0 ~ dunif(0, 100)
       x <- trunc(x0)
       q ~ dbeta(5,1)
       # LIKELIHOOD:
       # Estimation of probability of detection
       team1 ~ dbin(q, x)          # seen by team1
       team2 ~ dbin(q * (1-q), x) # missed by team1, seen by team2

       # Step 1. (N = number of plots at each site)
       for(i in 1:N) {
              z[i] ~ dbern(psi[zone.ID.ALL[i]])
              n[i] ~ dpois(lambda[zone.ID.ALL[i]] * a[i] * t[i] * z[i])
              y[i] ~ dbin(q, n[i])
       }
       # Step 2. (M = Study site in chronological survey order)
       for(M in 1:7) {
```

```
            psi[M] ~ dunif(0,1)
            lambda[M] ~ dunif(0,4)
            D.hat.ALL[M] <- lambda[M] * psi[M]
            d.hat.ALL[M] <- D.hat.ALL [M] / 0.8500  #  p.hat_r.hat  <-
0.8500
            mu.hat.ALL[M] <- d.hat.ALL[M] * Area.ALL[M]
      }
} ",fill = TRUE)
sink()
```

Before running `jags`, bundle the information from the data into: `JAGSdata.ALL` for compilation of vectors used by the model; `params.ALL` for a list of parameters of interest; and `inits.ALL` for the function to create initial values for the model.

```
JAGSdata.ALL <- with(nests.Data.ALL, list(z = any.sign.ALL,
      a = plot.size.ALL, zone.ID.ALL = zone.ID.ALL, y = nests.obs.ALL,
      Area.ALL = Area.ALL, t = period.ALL, N = nrow(nests.Data.ALL),
      team1 = 35, team2 = 5))
params.ALL <- c("psi", "lambda", "D.hat.ALL", "d.hat.ALL", "mu.hat.ALL",
      "q", "x0")
inits.ALL <- function() {list(lambda = rep(1, 7),
      n = nests.Data.ALL$nests.obs.ALL, x0 = 42, q = 0.9)}
```

Save the result as `JAGSout.ALL` after running `jags` with the specified Markov chain Monte Carlo (MCMC) settings.

```
# MCMC settings:
ni <- 40000
nt <- 2
nb <- 5000
nc <- 3

# JAGS output:
JAGSout.ALL <- jags(JAGSdata.ALL, inits.ALL, params.ALL,
      "model.txt", n.iter = ni, n.thin = nt, n.burnin = nb, n.chains =
nc)
```

Convert the MCMC output into `Bwiqid` class using the function `as.Bwiqid`. This Bayesian function converts different classes generated using WinBUGS, OpenBUGS or JAGS into a common class for printing and plotting using `wiqid`. The results for D.hat ($\hat{D}$), d.hat ($\hat{d}$), lambda ($\hat{\lambda}$), mu.hat ($\hat{\mu}$), and psi ($\hat{\psi}$) were numbered in chronological order of surveys at the seven study sites.

```
attach.jags(JAGSout.ALL)
out.ALL <- as.Bwiqid(JAGSout.ALL)
```

```
Model fitted in JAGS with R2jags
52500 simulations saved.
                mean       sd   median   HDIlo     HDIup  Rhat n.eff
D.hat.ALL1    1.1942  0.37382   1.1727  0.4624    1.9198 1.001 25000
D.hat.ALL2    1.5206  0.46010   1.5010  0.6326    2.4363 1.001 16000
D.hat.ALL3    0.3979  0.44065   0.2414  0.0000    1.3342 1.001 31000
D.hat.ALL4    0.1461  0.10052   0.1233  0.0068    0.3412 1.001 52000
D.hat.ALL5    0.8648  0.29218   0.8413  0.3130    1.4402 1.001 24000
D.hat.ALL6    0.7008  0.18764   0.6843  0.3444    1.0671 1.001  5900

D.hat.ALL7    0.1932  0.09799   0.1757  0.0369    0.3885 1.001 12000
d.hat.ALL1    1.4050  0.43979   1.3797  0.5440    2.2586 1.001 25000
d.hat.ALL2    1.7890  0.54130   1.7659  0.7442    2.8663 1.001 16000
d.hat.ALL3    0.4681  0.51841   0.2841  0.0000    1.5696 1.001 31000
d.hat.ALL4    0.1719  0.11826   0.1450  0.0080    0.4014 1.001 52000
d.hat.ALL5    1.0174  0.34375   0.9898  0.3682    1.6944 1.001 24000
d.hat.ALL6    0.8245  0.22075   0.8051  0.4052    1.2554 1.001  5900
d.hat.ALL7    0.2273  0.11529   0.2067  0.0436    0.4573 1.001 12000
deviance     79.4797 13.21313  78.6551 54.5287  105.9412 1.001  7500
lambda1       1.4905  0.34798   1.4559  0.8585    2.1889 1.001 17000
```

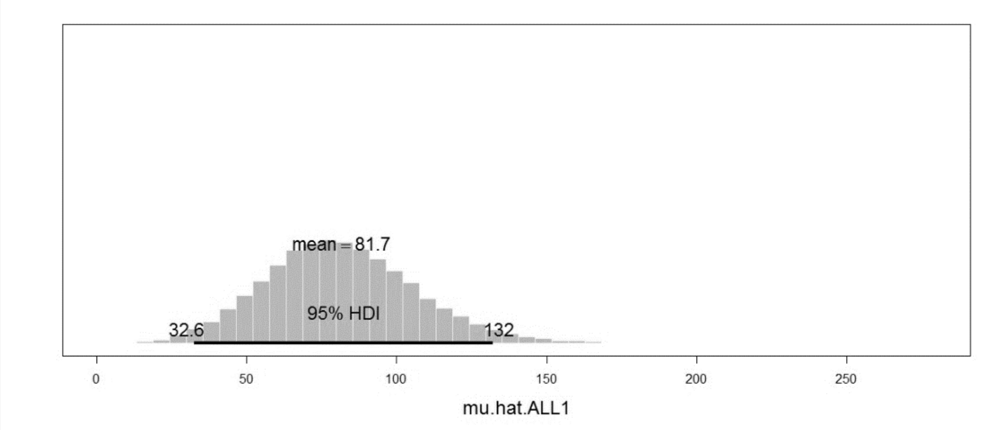
```
lambda2          1.9008  0.41771   1.8600  1.1421   2.7499 1.001  7900

lambda3          1.9988  1.15450   1.9997  0.0148   3.8142 1.001 52000
lambda4          0.2559  0.15097   0.2271  0.0273   0.5552 1.001 52000
lambda5          1.0814  0.28648   1.0501  0.5653   1.6554 1.001 18000
lambda6          0.8009  0.18754   0.7822  0.4636   1.1763 1.001  4600
lambda7          0.3082  0.13051   0.2893  0.0909   0.5735 1.001 12000
mu.hat.ALL1    81.8818 25.63090  80.4077 31.7023 131.6307 1.001 25000
mu.hat.ALL2    40.2157 12.16834  39.6974 16.7306  64.4334 1.001 16000
mu.hat.ALL3    32.4878 35.97737  19.7137  0.0000 108.9326 1.001 31000
mu.hat.ALL4    16.5699 11.40163  13.9802  0.7677  38.6970 1.001 52000
mu.hat.ALL5    46.6369 15.75731  45.3705 16.8790  77.6713 1.001 24000
mu.hat.ALL6   115.4335 30.90530 112.7106 56.7279 175.7626 1.001  5900
mu.hat.ALL7    56.3200 28.56812  51.2117 10.7618 113.2731 1.001 12000
psi1             0.8011  0.16271   0.8418  0.4765   1.0000 1.001 52000
psi2             0.8003  0.16360   0.8415  0.4743   1.0000 1.001 52000
psi3             0.1995  0.16343   0.1583  0.0000   0.5269 1.001 25000
psi4             0.5715  0.17582   0.5795  0.2403   0.9007 1.001 46000
psi5             0.8000  0.16354   0.8419  0.4699   1.0000 1.001 52000
psi6             0.8750  0.11051   0.9058  0.6497   1.0000 1.001 52000
psi7             0.6265  0.16042   0.6370  0.3250   0.9267 1.001 36000
q                0.8133  0.07534   0.8242  0.6588   0.9413 1.002  3600
x0              43.4237  4.60824  42.6675 36.0003  52.6110 1.001  4100

'HDIlo' and 'HDIup' are the limits of a 95% HDI credible interval.
'Rhat' is the potential scale reduction factor (at convergence, Rhat=1).
'n.eff' is a crude measure of effective sample size.
```

Objective #2: To generate histograms of the posterior outputs.

2.1. Estimated orangutan population (mu.hat)

Run the probability density function for mu.hat at each study site using the `plot` function. Histogram for each study site is generated by changing "mu.hat.ALL1" into "mu.hat.ALL2" ... up to "mu.hat.ALL7".

```
plot(out.ALL,   "mu.hat.ALL1",   showCurve=FALSE,   shadeHDI="skyblue",
xlim=c(0,280),       ylim=c(0,0.048))
```

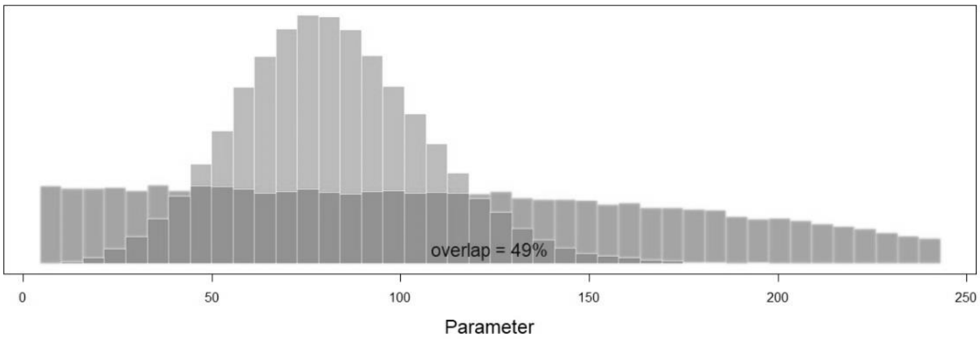


2.2. Estimated orangutan population (mu.hat) and comparison of percentage overlap between the posterior and prior distributions.

Use the function `postPriorOverlap` to check the percentage of posterior-prior overlap for each site. To compare other study sites, change "mu.hat.ALL[,1]" into "mu.hat.ALL[,2]"… up to "mu.hat.ALL[,7]".

```
# Step 3. Compare posterior-prior percentage overlap
JAGSdata.ALL$y <- NULL
JAGSout.ALL0  <- jags(JAGSdata.ALL, inits.ALL, params.ALL,
                    "model.txt",n.iter = ni, n.thin = nt, n.burnin = nb,
                    n.chains = nc)
```

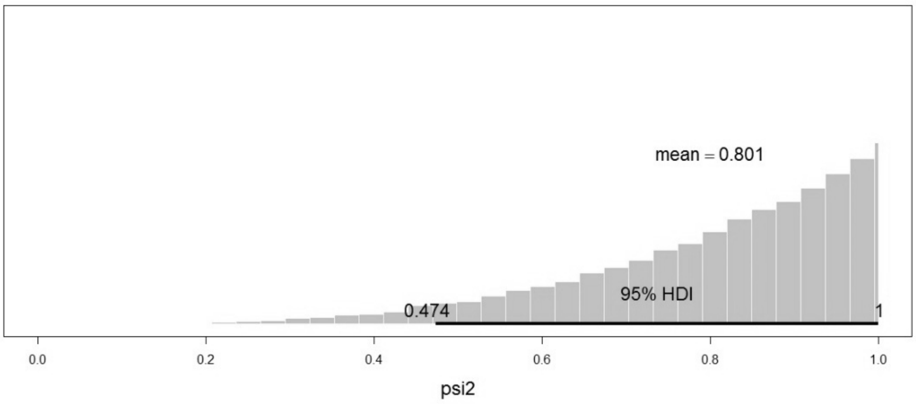
```
attach.jags(JAGSout.ALL)
postPriorOverlap(mu.hat.ALL[,1],
JAGSout.ALL0$BUGSoutput$sims.list$mu.hat.ALL[,1])
```



2.3. Estimated probability of old nest at a site (psi).

Generate the probability density function for each study site by changing “psi1” into “psi2” ... up to “psi7”.

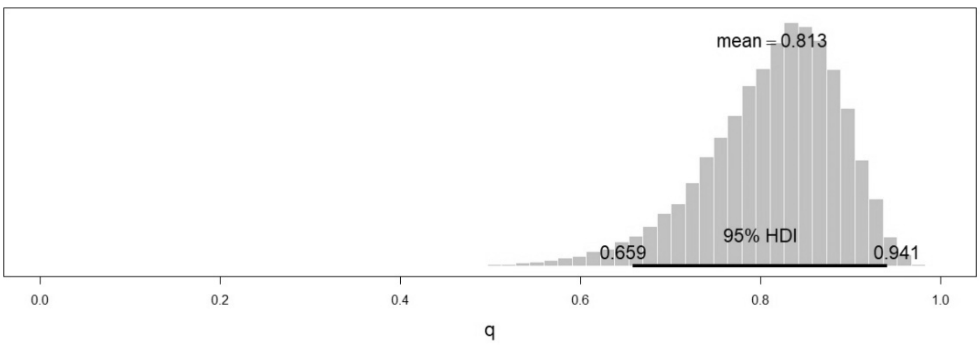
```
plot(out.ALL, "psi1", showCurve=FALSE, shadeHDI="skyblue", xlim=c(0,1),
       ylim=c(0,7))
```



2.4. Estimated probability of detecting new nest by the two teams on the first survey (*q*) with 95% HDI

Run the probability density function for *q* for all seven study sites using the `plot` function.

```
plot(out.ALL,  "q",  showCurve=FALSE,  shadeHDI="skyblue",  xlim=c(0,1),
       ylim=c(0,6))
```



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Chapter 4. Occupancy modelling of orangutan distribution at the greater Batang Ai-Lanjak-Entimau landscape in Sarawak, Malaysia

Supplementary Appendix S4.1. R script for occupancy estimation for individual tiles adapted from Panel 9.4 of Royle and Dorazio (2008). This R script was saved as 'SS_Spatial nests_new.txt' and sourced into the model to run in WinBUGS (Supplementary Appendix S4.3).

```
# Title: WinBUGS model specification for an auto-logistic model with
observation
#   of the state variable z subject to imperfect detection.
# Adapted from: Panel 9.4 of Royle & Dorazio (2008)

# Probability of occupancy for each site,
#   psi[i], is modelled as a logistic function of the proportion of
#     neighbouring sites occupied.
# The data consist of:
#   = nsite : total number of sites.
#   = y (vector) : the number of occasions on which new nest was
detected
#     at the tile; NA if the tile was not surveyed.
#   = K (vector) : the total number of survey occasions at each tile
#     (irrelevant if the tile was not surveyed, but must not be NA).
#   = NumNbrs (vector) : the number of neighbours for each tile.
#   = Nbrs (matrix) : tiles in rows; the first NumNbrs entries in each
#     row indicate which tiles neighbour the tile in questions.

model{

alpha ~ dnorm(0,.01)
beta ~ dnorm(0,.01)
p ~ dunif(0,1)

for(i in 1:nsite){
       x[i,1]<-0
       for(j in 1:NumNbrs[i]){
              x[i,j+1]<-x[i,j]+z[Nbrs[i,j]]
       }
       logit(psi[i])<- alpha + beta*(x[i,NumNbrs[i]+1]/NumNbrs[i])
       z[i]~dbern(psi[i])
       mu[i]<-z[i]*p
       y[i]~dbin(mu[i],K[i])
       }
}
```

Supplementary Appendix S4.2. R script to plot hexagonal tessellation. This R script was saved as ‘hexTess.R’ and sourced into Step 3 and 4 of the Supplementary Appendix S4.3. Mike Meredith (the main statistician of this study) wrote the original script.

```
# Title: Plot hexagonal tessellation.
# Written by: Mike Meredith (2017)

hexTess <- function(data, colors, horizontal=TRUE, border=NULL, ...) {
  # data : a data frame with the coordinates of the centres
  #  of the hexagons in the columns 1 and 2, and the values to plot in
  #  column 3.
  # colors : a vector of colour specifications
  # horizontal : if TRUE, the top and bottom sides of the hexagon are
  #  horizontal
  # border : colour of hexagon borders, NA = no border, NULL = default
  #  colour (black)
  # ... additional arguments for plotting functions (untested!)

  # Get together some basic info
  npix <- nrow(data)
  dist <- as.matrix(dist(data[, 1:2]))
  diag(dist) <- Inf
  rad <- min(dist) / (2 * cos(pi/6)) # distance from centre of hexagon
to
                                    #  vertices.
  rad <- rad * 1.01 # increase slightly to avoid gaps between hexagons
                    #  when plotted.

  # Get bounding box
  bbox <- data.frame(x = c(min(data[,1]) - rad, max(data[,1]) + rad),
                     y = c(min(data[,2]) - rad, max(data[,2]) + rad))

  # Determine what to add to centre coords to get vertices
  v1 <- c(-rad, -rad*cos(pi/3), rad*cos(pi/3), rad, rad*cos(pi/3),
         -rad*cos(pi/3))
  v2 <- c(0, rad*sin(pi/3), rad*sin(pi/3), 0, -rad*sin(pi/3), -
rad*sin(pi/3))
  if(horizontal) {
    vX <- v1 ; vY <- v2
  } else {
    vX <- v2 ; vY <- v1
  }

  # Create array with coordinates of vertices: 6 x 2 x npix
  verts <- array(NA, dim=c(6, 2, npix))
  verts[, 1, ] <- outer(vX, data[,1], FUN="+")
  verts[, 2, ] <- outer(vY, data[,2], FUN="+")

  # Get the colours to plot
  ncolors <- length(colors)
  # scale z to range [0, 1]
  tmp <- data[, 3] - min(data[, 3])
  z <- tmp / max(tmp)
  zcols <- floor(z * (ncolors-1)) + 1
  # zcols[zcols > ncolors] <- ncolors # doesn't seem to be needed

  op <- par(mar=c(5,4,4,6)+0.1) ; on.exit(par(op))
  MASS::eqscplot(bbox, type="n", bty="n", xlab="", ylab="", ...)
  for(i in 1:npix)
    polygon(verts[, , i], border=border, col=colors[zcols[i]], ...)

  AHMbook::image_scale(data[,3], colors, digits=2)

  return(invisible(verts))
}
```

Supplementary Appendix S4.3. Main R script to run the analysis and source codes from Supplementary Appendix S4.1 and S4.2. Mike Meredith (the main statistician of this study) wrote the original script.

```
# Title: Main R script to run orangutan occupancy probability paper.
# Written by: Mike Meredith (2017)

library(R2WinBUGS)
raw <- read.csv("new_nests_spatial.csv", row.names=1)
attach(raw)

#   = raw : data frame of new nest data imported via read.csv
#   The variables in the data frame are:
#   = Tile : original code for main hexagonal tiles
#   = East : easting, Coordinate System: Borneo RSO Timbalai 1948
#   = North : northing, Coordinate System: Borneo RSO Timbalai 1948
#   = K : number of visits to each plot (9 if not surveyed)
#   = Surveyed : 1 = surveyed, 0 = not surveyed
#   = Nestnew : number of visits when nest was recorded,
#      blank (NA) if not surveyed.

# Step 1.Do a matrix with pair-wise distances between tiles
# ==========================================================
coords <- raw[, 1:2]
dist <- as.matrix(dist(coords))
# Put Inf on the diagonal (otherwise tile is its own neighbour)
diag(dist) <- Inf
# Check - look at neighbours for point #1
pt1 <- which(dist[1, ] < 3160)
# function to get neighbours for 1 column of dist
getNeigh <- function(x) {
  tmp <- which(x < 3160)
  return(c(tmp, rep(NA, 6 - length(tmp))))
}

Nbrs <- t(apply(dist, 2, getNeigh))
dim(Nbrs)
head(Nbrs)

# See how many neighbours each sub-tile has:
NumNbrs <- rowSums(!is.na(Nbrs))
min(NumNbrs) # None less than 2


# Step 2.Run model in WinBUGS
# ===========================
ntiles <- nrow(raw)
# Set up data for WinBUGS:
bugdat <- list(
   y = Nestnew,
   nsite = ntiles,
   K = K,
   NumNbrs = NumNbrs,
   Nbrs = Nbrs)
str(bugdat)
pars <- c("p", "alpha", "beta", "psi", "z")

# The main run (takes ca. 10 mins):
spat1 <- bugs(bugdat, NULL, pars, "SS_Spatial nests_new.txt",
         n.chain=2, n.burn=5000, n.iter=25000, debug=TRUE)
# bugs.run.time()

spat1$mean$p # Mean probability of detection
# Put mean values for occupancy into a separate vector:
z <- spat1$mean$z
```

```
# Step 3.Generate map of posterior mean occupancy probability of
orangutans
#
===========================================================================
===
psi <- spat1$mean$psi
psicol <- round(psi*10)+1
colorz <- rev(grey.colors(5))

source("hexTess.R")
hexTess(cbind(raw[, 1:2], psi), colorz, border="grey")
title(main="Posterior mean of occupancy probability of new
             orangutan nest at the greater BALE landscape",
       xlab="East", ylab="North", cex=1.5, las=1,
       sub="Coordinate systems: Borneo RSO Timbalai 1948 (EPSG:
29873)")


# Step 4.Generate map of posterior CV of occupancy probability
# ============================================================
psi.sd <- spat1$sd$psi
psi.CV <- spat1$sd$psi / spat1$mean$psi
colorz.se <- rev(grey.colors(5)) # new colours
hexTess(cbind(raw[, 1:2], psi.CV), colorz.se, border="grey") # with
borders
title(main="Posterior CV of occupancy probability
             of new orangutan nest at the greater BALE landscape",
       xlab="East", ylab="North", cex=1.5, las=1,
       sub="Coordinate systems: Borneo RSO Timbalai 1948 (EPSG:
29873)")
```